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Cockroach

Cockroaches are insects of the order Blattodea, which also includes termites. About 30 cockroach species out of 4,600 are associated with human habitats. About four species are well known as pests.

The cockroaches are an ancient group, dating back at least as far as the Carboniferous period, some 320 million years ago. Those early ancestors however lacked the internal ovipositors of modern roaches. Cockroaches are somewhat generalized insects without special adaptations like the sucking mouthparts of aphids and other true bugs; they have chewing mouthparts and are likely among the most primitive of living neopteran insects. They are common and hardy insects, and can tolerate a wide range of environments from Arctic cold to tropical heat. Tropical cockroaches are often much bigger than temperate species, and, contrary to popular belief, extinct cockroach relatives and 'roachoids' such as the Carboniferous *Archimylacris* and the Permian *Apthoroblattina* were not as large as the biggest modern species.

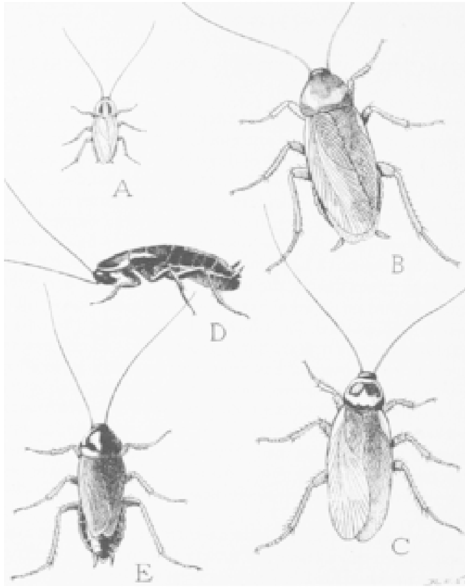
Some species, such as the gregarious German cockroach, have an elaborate social structure involving common shelter, social dependence, information transfer and kin recognition. Cockroaches have appeared in human culture since classical antiquity. They are popularly depicted as dirty pests, though the great majority of species are inoffensive and live in a wide range of habitats around the world.

Cockroach

Temporal range: 145–0 Ma

PreЄ Є O S D C P T J K PgN

Cretaceous–recent



Common household cockroaches

A) German cockroach

B) American cockroach

C) Australian cockroach

D&E) Oriental cockroach (♀ & ♂)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Dictyoptera
Order:	Blattodea

Families

Blaberidae
Blattidae
Corydiidae
Cryptocercidae
Ectobiidae
Lamproblattidae
Nocticolidae
Tryonicidae

Contents

Taxonomy and evolution

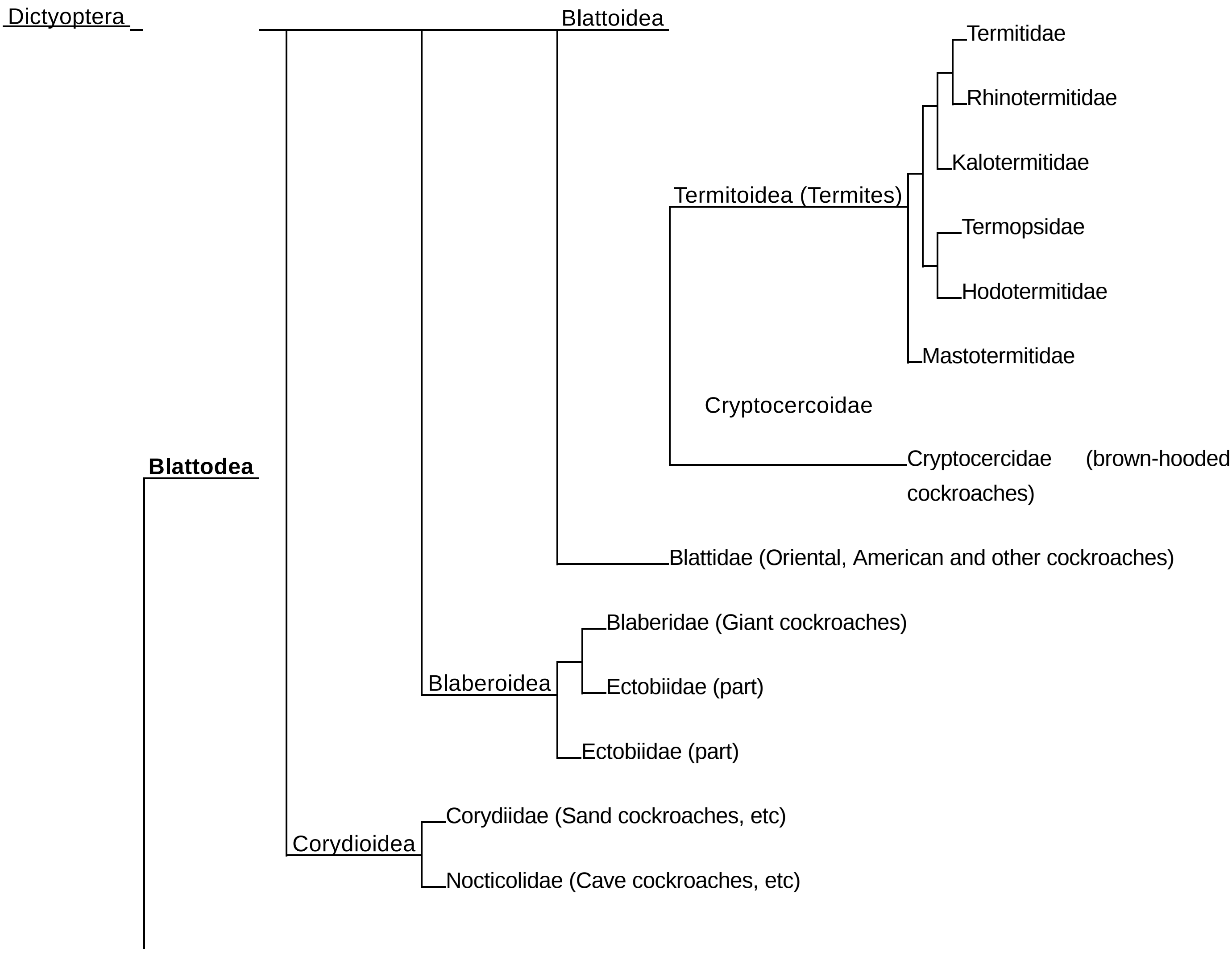
A 40- to 50-million-year-old cockroach in Baltic amber (Eocene)

Cockroaches are members of the order Blattodea, which includes the termites, a group of insects once thought to be separate from cockroaches. Currently, 4,600 species and over 460 genera are described worldwide.[1][2] The name "cockroach" comes from the Spanish word for cockroach, *cucaracha*, transformed by 1620s English folk etymology into "cock" and "roach".[3] The scientific name derives from the Latin *blatta*, "an insect that shuns the light", which in classical Latin was applied to not only cockroaches, but also mantids.[4][5]

Historically, the name Blattaria was used largely interchangeably with the name Blattodea, but whilst the former name was used to refer to 'true' cockroaches exclusively, the latter also includes the termites. The current catalogue of world cockroach species uses the name Blattodea for the group.[1] Another name, Blattoptera, is also sometimes used.[6] The earliest cockroach-like fossils ("blattopterans" or "roachids") are from the Carboniferous period 320 million years ago, as are fossil roachoid nymphs.[7][8][9]

Since the 19th century, scientists believed that cockroaches were an ancient group of insects that had a Devonian origin, according to one hypothesis.[10] Fossil roachoids that lived during that time differ from modern cockroaches in having long external ovipositors and are the ancestors of mantises, as well as modern blattodeans. As the body, hind wings and mouthparts are not preserved in fossils frequently, the relationship of these roachoids and modern cockroaches remains disputed. The first fossils of modern cockroaches with internal ovipositors appeared in the early Cretaceous. A recent phylogenetic analysis suggests that cockroaches originated at least in the Jurassic.[10]

The evolutionary relationships of the Blattodea (cockroaches and termites) shown in the cladogram are based on Eggleton, Beccaloni & Inward (2007).[11] The cockroach families Lamproblattidae and Tryonicidae are not shown but are placed within the superfamily Blattoidea. The cockroach families Corydiidae and Ectobiidae were previously known as the Polyphagidae and Blattellidae.[12]



Mantodea (Mantises)

Termites were previously regarded as a separate order Isoptera to cockroaches. However, recent genetic evidence strongly suggests that they evolved directly from 'true' cockroaches, and many authors now place them as an "epifamily" of Blattodea.[11] This evidence supported a hypothesis suggested in 1934 that termites are closely related to the wood-eating cockroaches (genus *Cryptocercus*). This hypothesis was originally based on similarity of the symbiotic gut flagellates in termites regarded as living fossils and wood-eating cockroaches.[13] Additional evidence emerged when F. A. McKittrick (1965) noted similar morphological characteristics between some termites and cockroach nymphs.[14] The similarities among these cockroaches and termites have led some scientists to reclassify termites as a single family, the Termitidae, within the order Blattodea.[11][15] Other scientists have taken a more conservative approach, proposing to retain the termites as the Termitoidea, an epifamily within the order. Such measure preserves the classification of termites at family level and below.[16]

Description

Domino cockroach *Therea petiveriana*, normally found in India

Most species of cockroach are about the size of a thumbnail, but several species are bigger. The world's heaviest cockroach is the Australian giant burrowing cockroach *Macropanesthia rhinoceros*, which can reach 9 cm (3.5 in) in length and weigh more than 30 g (1.1 oz).[17] Comparable in size is the Central American giant cockroach *Blaberus giganteus*, which grows to a similar length.[18] The longest cockroach species is *Megaloblatta longipennis*, which can reach 97 mm (3.8 in) in length and 45 mm (1.8 in) across.[19] A Central and South American species, *Megaloblatta blaberoides*, has the largest wingspan of up to 185 mm (7.3 in).[20]

Head of *Periplaneta americana*

Cockroaches are generalized insects, with few special adaptations, and may be among the most primitive living neopteran insects. They have a relatively small head and a broad, flattened body, and most species are reddish-brown to dark brown. They have large compound eyes, two ocelli, and long, flexible antennae. The mouthparts are on the underside of the head and include generalized chewing mandibles, salivary glands and various touch and taste receptors.[21]

The body is divided into a thorax of three segments and a ten-segmented abdomen. The external surface has a tough exoskeleton which contains calcium carbonate and protects the inner organs and provides attachment to muscles. It is coated with wax to repel water. The wings are attached to the second and third thoracic segments. The tegmina, or first pair of wings, are tough and protective, lying as a shield on top of the membranous hind wings, which are used in flight. All four wings have branching longitudinal veins, and multiple cross-veins.[22]

The three pairs of legs are sturdy, with large coxae and five claws each.[22] They are attached to each of the three thoracic segments. The front legs are the shortest and the hind legs the longest, providing the main propulsive power when the insect runs.[21] The spines on the legs were earlier considered to be sensory, but observations of the insect's gait on sand and wire meshes have demonstrated that they help in locomotion on difficult terrain. The structures have been used as inspiration for robotic legs.[23][24]

The abdomen has ten segments, each with a pair of spiracles for respiration. Segment ten bears a pair of cerci, a pair of anal styles, the anus and the external genitalia. Males have an aedeagus through which they secrete sperm during copulation and females have spermathecae for storing sperm and an ovipositor through which the ootheca is laid.[21]

Distribution and habitat

Cockroaches are abundant throughout the world and live in a wide range of environments, especially in the tropics and subtropics.[25] Cockroaches can withstand extremely cold temperatures, allowing them to live in the Arctic. Some species are capable of surviving temperatures of −188 °F (−122 °C) by manufacturing an antifreeze made out of glycerol.[26] In North America, 50 species separated into

five families are found throughout the continent.[25] 450 species are found in Australia.[27] Only about four widespread species are commonly regarded as pests.[28][29]

Cockroaches occupy a wide range of habitats. Many live in leaf litter, among the stems of matted vegetation, in rotting wood, in holes in stumps, in cavities under bark, under log piles and among debris. Some live in arid regions and have developed mechanisms to survive without access to water sources. Others are aquatic, living near the surface of water bodies, including bromeliad phytotelmata, and diving to forage for food. Most of these respire by piercing the water surface with the tip of the abdomen which acts as a snorkel, but some carry a bubble of air under their thoracic shield when they submerge. Others live in the forest canopy where they may be one of the main types of invertebrate present. Here they may hide during the day in crevices, among dead leaves, in bird and insect nests or among epiphytes, emerging at night to feed.[30]

Behavior

A cockroach soon after ecdysis

Cockroaches are social insects; a large number of species are either gregarious or inclined to aggregate, and a slightly smaller number exhibit parental care.[31] It used to be thought that cockroaches aggregated because they were reacting to environmental cues, but it is now believed that pheromones are involved in these behaviors. Some species secrete these in their feces with gut microbial symbionts being involved, while others use glands located on their mandibles. Pheromones produced by the cuticle may enable cockroaches to distinguish between different populations of cockroach by odor. The behaviors involved have been studied in only a few species, but German cockroaches leave fecal trails with an odor gradient.[31] Other cockroaches follow such trails to discover sources of food and water, and where other cockroaches are hiding. Thus, cockroaches have emergent behavior, in which group or swarm behavior emerges from a simple set of individual interactions.[32]

Daily rhythms may also be regulated by a complex set of hormonal controls of which only a small subset have been understood. In 2005, the role of one of these proteins, pigment dispersing factor (PDF), was isolated and found to be a key mediator in the circadian rhythms of the cockroach.[33]

Pest species adapt readily to a variety of environments, but prefer warm conditions found within buildings. Many tropical species prefer even warmer environments. Cockroaches are mainly nocturnal[34] and run away when exposed to light. An exception to this is the Asian cockroach, which flies mostly at night but is attracted to brightly lit surfaces and pale colors.[35]

Collective decision-making

Gregarious cockroaches display collective decision-making when choosing food sources. When a sufficient number of individuals (a "quorum") exploits a food source, this signals to newcomer cockroaches that they should stay there longer rather than leave for elsewhere.[36] Other mathematical models have been developed to explain aggregation dynamics and conspecific recognition.[37][38]

Cooperation and competition are balanced in cockroach group decision-making behavior.[32]

Cockroaches appear to use just two pieces of information to decide where to go, namely how dark it is and how many other cockroaches there are. A study used specially-scented roach-sized robots that appear to the roaches as real to demonstrate that once there are enough insects in a place to form a critical mass, the roaches accepted the collective decision on where to hide, even if this was an unusually lit place.[39]

Social behavior

When reared in isolation, German cockroaches show behavior that is different from behavior when reared in a group. In one study, isolated cockroaches were less likely to leave their shelters and explore, spent less time eating, interacted less with conspecifics when exposed to them, and took longer to recognize receptive females. Because these changes occurred in many contexts, the authors suggested them as constituting a behavioral syndrome. These effects might have been due either to reduced metabolic and developmental rates in isolated individuals or the fact that the isolated individuals hadn't had a training period to learn about what others were like via their antennae.[40]

Individual American cockroaches appear to have consistently different "personalities" regarding how they seek shelter. In addition, group personality is not simply the sum of individual choices, but reflects conformity and collective decision-making.[41][42]

The gregarious German and American cockroaches have elaborate social structure, chemical signalling, and "social herd" characteristics. Lihoreau and his fellow researchers stated:[32]

> The social biology of domiciliary cockroaches ... can be characterized by a common shelter, overlapping generations, non-closure of groups, equal reproductive potential of group members, an absence of task specialization, high levels of social dependence, central place foraging, social information transfer, kin recognition, and a meta-population structure.[32]

Sounds

Some species make a hissing noise while other cockroaches make a chirping noise. The Madagascar hissing cockroach produces its sound through the modified spiracles on the fourth abdominal segment. Several different hisses are produced, including disturbance sounds, produced by adults and larger nymphs; and aggressive, courtship and copulatory sounds produced by adult males.[43] *Henschoutedenia epilamproides* has a stridulatory organ between its thorax and abdomen, but the purpose of the sound produced is unclear.[44]

Several Australian species practice acoustic and vibration behavior as an aspect of courtship. They have been observed producing hisses and whistles from air forced through the spiracles. Furthermore, in the presence of a potential mate, some cockroaches tap the substrate in a rhythmic, repetitive manner. Acoustic signals may be of greater prevalence amongst perching species, particularly those that live on low vegetation in Australia's tropics.[45]

Biology

Digestive tract

Cockroaches are generally omnivorous; the American cockroach (*Periplaneta americana*), for example, feeds on a great variety of foodstuffs including bread, fruit, leather, starch in book bindings, paper, glue, skin flakes, hair, dead insects and soiled clothing.[46] Many species of cockroach harbor in their gut symbiotic protozoans and bacteria which are able to digest cellulose. In many species, these symbionts may be essential if the insect is to utilize cellulose; however, some species secrete cellulase in their saliva, and the wood-eating cockroach, *Panesthia cribrata*, is able to survive indefinitely on a diet of crystallized cellulose while being free of micro-organisms.[47]

The similarity of these symbionts in the genus *Cryptocercus* to those in termites are such that these cockroaches have been suggested to be more closely related to termites than to other cockroaches,[48] and current research strongly supports this hypothesis about their relationships.[49] All species studied so far carry the obligate mutualistic endosymbiont bacterium *Blattabacterium*, with the exception of *Nocticola australiensise*, an Australian cave-dwelling species without eyes, pigment or wings, which recent genetic studies indicate is a very primitive cockroach.[50][51] It had previously been thought that all five families of cockroach were descended from a common ancestor that was infected with *B. cuenoti*. It may be that *N. australiensise* subsequently lost its symbionts, or alternatively this hypothesis will need to be re-examined.[51]

Tracheae and breathing

Like other insects, cockroaches breathe through a system of tubes called tracheae which are attached to openings called spiracles on all body segments. When the carbon dioxide level in the insect rises high enough, valves on the spiracles open and carbon dioxide diffuses out and oxygen diffuses in. The tracheal system branches repeatedly, the finest tracheoles bringing air directly to each cell, allowing gaseous exchange to take place.[52]

While cockroaches do not have lungs as do vertebrates, and can continue to respire if their heads are removed, in some very large species, the body musculature may contract rhythmically to forcibly move air in and out of the spiracles; this may be considered a form of breathing.[52]

Reproduction

Cockroaches use pheromones to attract mates, and the males practice courtship rituals, such as posturing and stridulation. Like many insects, cockroaches mate facing away from each other with their genitalia in contact, and copulation can be prolonged. A few species are known to be parthenogenetic, reproducing without the need for males.[22]

Female cockroaches are sometimes seen carrying egg cases on the end of their abdomens; the German cockroach holds about 30 to 40 long, thin eggs in a case called an ootheca. She drops the capsule prior to hatching, though live births do occur in rare instances. The egg capsule may take more than five hours to lay and is initially bright white in color. The eggs are hatched from the combined pressure of the hatchlings gulping air. The hatchlings are initially bright white nymphs and continue inflating themselves with air, becoming harder and darker within about four hours. Their transient white stage while hatching and later while molting has led to claims of albino cockroaches.[22] Development from eggs to adults takes three to four months. Cockroaches live up to a year, and the female may produce up to eight egg cases in a lifetime; in favorable conditions, she can produce 300 to 400 offspring. Other species of cockroaches, however, can produce far more eggs; in some cases a female needs to be impregnated only once to be able to lay eggs for the rest of her life.[22]

The female usually attaches the egg case to a substrate, inserts it into a suitably protective crevice, or carries it about until just before the eggs hatch. Some species, however, are ovoviviparous, keeping the eggs inside their body, with or without an egg case, until they hatch. At least one genus, *Diploptera*, is fully viviparous.[22]

Cockroaches have incomplete metamorphosis, meaning that the nymphs are generally similar to the adults, except for undeveloped wings and genitalia. Development is generally slow, and may take a few months to over a year. The adults are also long-lived, and have survived for as much as four years in the laboratory.[22]

3 millimeter cockroach nymph

Female *Periplaneta fuliginosa* with ootheca

Empty ootheca

American cockroach oothecae

Hardiness

Cockroaches are among the hardiest insects. Some species are capable of remaining active for a month without food and are able to survive on limited resources, such as the glue from the back of postage stamps.[53] Some can go without air for 45 minutes. Japanese cockroach (*Periplaneta japonica*) nymphs, which hibernate in cold winters, survived twelve hours at −5 °C to −8 °C in laboratory experiments.[54]

Experiments on decapitated specimens of several species of cockroach found a variety of behavioral functionality remained, including shock avoidance and escape behavior, although many insects other than cockroaches are also able to survive decapitation, and popular claims of the longevity of headless cockroaches do not appear to be based on published research.[55][56] The severed head is able to survive and wave its antennae for several hours, or longer when refrigerated and given nutrients.[56]

It is popularly suggested that cockroaches will "inherit the earth" if humanity destroys itself in a nuclear war. Cockroaches do indeed have a much higher radiation resistance than vertebrates, with the lethal dose perhaps six to 15 times that for humans. However, they are not exceptionally radiation-resistant compared to other insects, such as the fruit fly.[57]

The cockroach's ability to withstand radiation better than human beings can be explained through the cell cycle. Cells are most vulnerable to the effects of radiation when they are dividing. A cockroach's cells divide only once each time it molts, which is weekly at most in a juvenile roach. Since not all cockroaches would be molting at the same time, many would be unaffected by an acute burst of radiation, although lingering radioactive fallout would still be harmful.[52]

Relationship with humans

In research and education

Cockroaches in research: *Periplaneta americana* in an electrophysiology experiment

Because of their ease of rearing and resilience, cockroaches have been used as insect models in the laboratory, particularly in the fields of neurobiology, reproductive physiology and social behavior.[31] The cockroach is a convenient insect to study as it is large and simple to raise in a laboratory environment. This makes it suitable both for research and for school and undergraduate biology studies. It can be used in experiments on topics such as learning, sexual pheromones, spatial orientation, aggression, activity rhythms and the biological clock, and behavioral ecology.[58] Research conducted in 2014 suggests that humans fear cockroaches the most, even more than mosquitoes, due to an evolutionary aversion.[59]

As pests

The Blattodea include some thirty species of cockroaches associated with humans; these species are atypical of the thousands of species in the order.[60] They feed on human and pet food and can leave an offensive odor.[61] They can passively transport pathogenic microbes on their body surfaces, particularly in environments such as hospitals.[62][63] Cockroaches are linked with allergic reactions in humans.[64][65] One of the proteins that trigger allergic reactions is tropomyosin.[66] These allergens are also linked with asthma.[67] About 60% of asthma patients in Chicago are also sensitive to cockroach allergens. Studies similar to this have been done globally and all the results are similar. Cockroaches can live for a few days up to a month without food, so just because no cockroaches are visible in a home does not mean they are not there. Approximately 20-48% of homes with no visible sign of cockroaches have detectable cockroach allergens in dust.[68]

Cockroaches can burrow into human ears, causing pain and hearing loss.[69][70] They may be removed with forceps, possibly after first drowning with olive oil.[71][72][73]

Control

Many remedies have been tried in the search for control of the major pest species of cockroaches, which are resilient and fast-breeding. Household chemicals like sodium bicarbonate (baking soda) have been suggested, without evidence for their effectiveness.[74] Garden herbs including bay, catnip, mint, cucumber, and garlic have been proposed as repellents.[75] Poisoned bait containing hydramethylnon or fipronil, and boric acid powder is effective on adults.[76] Baits with egg killers are also quite effective at reducing the cockroach population. Alternatively, insecticides containing deltamethrin or pyrethrin are very effective.[76] In Singapore and Malaysia, taxi drivers use pandan leaves to repel cockroaches in their vehicles.[77]

Few parasites and predators are effective for biological control of cockroaches. Parasitoidal wasps such as *Ampulex* wasps sting nerve ganglia in the cockroach's thorax, temporarily paralyzing the victim, allowing the wasp to deliver an incapacitating sting into the cockroach's brain. The wasp clips the antennae with its mandibles and drinks some hemolymph before dragging the prey to a burrow, where an egg (rarely two) is laid on it.[78] The wasp larva feeds on the subdued living cockroach.[79][80] Another wasp which is considered a promising candidate for biological control is the ensign wasp *Evania appendigaster* which attacks cockroach oothecae to lay a single egg inside.[81][82] Ongoing research is still developing technologies allowing for mass-rearing these wasps for application releases.[83][84]

Cockroaches can be trapped in a deep, smooth-walled jar baited with food inside, placed so that cockroaches can reach the opening, for example with a ramp of card or twigs on the outside. An inch or so of water or stale beer (by itself a cockroach attractant) in the jar can be used to drown any insects thus captured. The method works well with the American cockroach, but less so with the German cockroach.[85]

A study conducted by scientists at Purdue University concluded that the most common cockroaches in the US, Australia and Europe were able to develop a “cross resistance” to multiple types of pesticide. This contradicted previous understanding that the animals can develop resistance against one pesticide at a time.[86] The scientists suggested that cockroaches will no longer be easily controlled using a diverse spectrum of chemical pesticides and that a mix of other means, such as traps and better sanitation, will need to be employed.[87]

As food

Although considered disgusting in Western culture, cockroaches are eaten in many places around the world.[88][89] Whereas household pest cockroaches may carry bacteria and viruses, cockroaches bred under laboratory conditions can be used to prepare nutritious food.[90] In Mexico and Thailand, the heads and legs are removed, and the remainder may be boiled, sautéed, grilled, dried or diced.[88] In China, cockroaches have become popular as medicine and cockroach farming is rising with over 100 farms.[91] The cockroaches are fried twice in a wok of hot oil, which makes them crispy with soft innards that are like cottage cheese.[92][93] Fried cockroaches are ground and sold as pills for stomach, heart and liver diseases.[94] A cockroach recipe from Formosa (Taiwan) specifies salting and frying cockroaches after removing the head and entrails.[95]

In traditional and homeopathic medicine

In China, cockroaches are raised in large quantities for medicinal purposes.[96]

Two species of cockroach were used in homeopathic medicine in the 19th century.[97]

Conservation

While a small minority of cockroaches are associated with human habitats and viewed as repugnant by many people, a few species are of conservation concern. The Lord Howe Island wood-feeding cockroach (*Panesthia lata*) is listed as endangered by the New South Wales Scientific Committee, but the cockroach may be extinct on Lord Howe Island itself. The introduction of rats, the spread of Rhodes grass (*Chloris gayana*) and fires are possible reasons for their scarcity.[98] Two species are currently listed as endangered and critically endangered by the IUCN Red List, *Delosia ornata* and *Nocticola gerlachi*.[99][100] Both cockroaches have a restricted distribution and are threatened by habitat loss and rising sea levels. Only 600 *Delosia ornata* adults and 300 nymphs are known to exist, and these are threatened by a hotel development. No action has been taken to save the two cockroach species, but protecting their natural habitats may prevent their extinction. In the former Soviet Union, cockroach populations have been declining at an alarming rate; this may be exaggerated, or the phenomenon may be temporary or cyclic.[101] One species of roach, *Simandoa conserfariam*, is considered extinct in the wild.

Cultural depictions

Cockroaches were known and considered repellent but useful in medicines in Classical times. An insect named in Greek "σίλφη" (*silphe*) has been identified with the cockroach. It is mentioned by Aristotle, saying that it sheds its skin; it is described as foul-smelling in Aristophanes' play *Peace*; Euenus called it a pest of book collections, being "page-eating, destructive, black-bodied" in his *Analect*. Virgil named the cockroach "Lucifuga" ("one that avoids light"). Pliny the Elder recorded the use of "Blatta" in various medicines; he describes the insect as disgusting, and as seeking out dark corners to avoid the light.[102][103] Dioscorides recorded the use of the "Silphe", ground up with oil, as a remedy for earache.[103]

Madagascar hissing cockroaches kept as pets

Lafcadio Hearn (1850–1904) asserted that "For tetanus cockroach tea is given. I do not know how many cockroaches go to make up the cup; but I find that faith in this remedy is strong among many of the American population of New Orleans. A poultice of boiled cockroaches is placed over the wound." He adds that cockroaches are eaten, fried with garlic, for indigestion.[104]

Several cockroach species, such as *Blaptica dubia*, are raised as food for insectivorous pets.[105] A few cockroach species are raised as pets, most commonly the giant Madagascar hissing cockroach, *Gromphadorhina portentosa*.[106] Whilst the hissing cockroaches may be the most commonly kept species, there are many species that are kept by cockroach enthusiasts; there is even a specialist society: the Blattodea Culture Group (BCG), which was a thriving organisation for about 15 years although now appears to be dormant.[107] The BCG provided a source of literature for people interested in rearing cockroaches which was otherwise limited to either scientific papers, or general insect books, or books covering a variety of exotic pets; in the absence of an inclusive book one member published *Introduction to Rearing Cockroaches* which still appears to be the only book dedicated to rearing cockroaches.[108]

Cockroaches have been used for space tests. A cockroach given the name Nadezhda was sent into space by Russian scientists as part of a Foton-M mission, during which she mated, and later became the first terrestrial animal to produce offspring that had been conceived in space.[109]

Because of their long association with humans, cockroaches are frequently referred to in popular culture. In Western culture, cockroaches are often depicted as dirty pests.[110][111] In a 1750–1752 journal, Peter Osbeck noted that cockroaches were frequently seen and found their way to the bakeries, after the sailing ship *Gothenburg* ran aground and was destroyed by rocks.[112]

Donald Harington's satirical novel *The Cockroaches of Stay More* (Harcourt, 1989) imagines a community of "roosterroaches" in a mythical Ozark town where the insects are named after their human counterparts. Madonna has famously quoted, "I am a survivor. I am like a cockroach, you just can't get rid of me."[113] An urban legend maintains that cockroaches are immortal.[114]

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Housefly

The **housefly** (*Musca domestica*) is a fly of the suborder Cyclorrhapha. It is believed to have evolved in the Cenozoic era, possibly in the Middle East, and has spread all over the world as a commensal of humans. It is the most common fly species found in houses. Adults are grey to black, with four dark, longitudinal lines on the thorax, slightly hairy bodies, and a single pair of membranous wings. They have red eyes, set farther apart in the slightly larger female.

The female housefly usually mates only once and stores the sperm for later use. She lays batches of about 100 eggs on decaying organic matter such as food waste, carrion, or feces. These soon hatch into legless white larvae, known as maggots. After 2 to 5 days of development, these metamorphose into reddish-brown pupae, about 8 mm (0.3 in) long. Adult flies normally live for 2 to 4 weeks, but can hibernate during the winter. The adults feed on a variety of liquid or semiliquid substances, as well as solid materials which have been softened by their saliva. They can carry pathogens on their bodies and in their faeces, contaminate food, and contribute to the transfer of food-borne illnesses, while, in numbers, they can be physically annoying. For these reasons, they are considered pests.

Houseflies have been used in the laboratory in research into aging and sex determination. Flies appear in literature from Ancient Greek myth and Aesop's *The Impertinent Insect* onwards. Authors sometimes choose the fly to speak of the brevity of life, as in William Blake's 1794 poem "The Fly", which deals with mortality subject to uncontrollable circumstances.

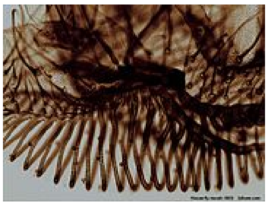
Housefly	
	
Conservation status	
Not evaluated (IUCN 3.1)	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Diptera
Section:	Schizophora
Family:	Muscidae
Genus:	*Musca*
Species:	***M. domestica***
Binomial name	
Musca domestica Linnaeus, 1758	
Subspecies	
▪ *M. d. calleva* Walker, 1849	
▪ *M. d. domestica* Linnaeus, 1758	

Contents

Description

Head of a female housefly with two large compound eyes and three ocelli

Adult houseflies are usually 6 to 7 mm (0.24 to 0.28 in) long with a wingspan of 13 to 15 mm (0.5 to 0.6 in). The females tend to be larger winged than males, while males have relatively longer legs. Females tend to vary more in size[1] and there is geographic variation with larger individuals in higher latitudes.[2] The head is strongly convex in front and flat and slightly conical behind. The pair of large compound eyes almost touch in the male, but are more widely separated in the female. They have three simple eyes (ocelli) and a pair of short antennae.[3] Flies process visual information around seven times more quickly than humans, enabling them to identify and avoid attempts to catch or swat them, since they effectively see the human's movements in slow motion with their higher flicker fusion rate.[4][5]

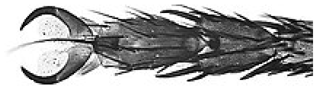


Mouthparts, showing the pseudotracheae, semitubular grooves (dark parallel bands) used for sucking up liquid food

The mouthparts are specially adapted for a liquid diet; the mandibles and maxillae are reduced and not functional, and the other mouthparts form a retractable, flexible proboscis with an enlarged, fleshy tip, the labellum. This is a sponge-like structure that is characterised by many grooves, called pseudotracheae, which suck up fluids by capillary action.[6][7] It is also used to distribute saliva to soften solid foods or collect loose particles.[8] Houseflies have chemoreceptors, organs of taste, on the tarsi of their legs, so they can identify foods such as sugars by walking over them.[9] Flies are often seen cleaning their legs by rubbing them together, enabling the chemoreceptors to taste afresh whatever they walk on next.[10] At the end of each leg is a pair of claws, and below them are two adhesive pads, pulvilli, enabling the fly to walk up smooth walls and ceilings using Van der Waals forces. The claws help the fly to unstick the foot for the next step. Flies walk with a common gait on horizontal and vertical surfaces with three legs in contact with the surface and three in movement. On inverted surfaces, they alter the gait to keep four feet stuck to the surface.[11] Flies land on a ceiling by flying straight towards it; just before landing, they make a half roll and point all six legs at the surface, absorbing the shock with the front legs and sticking a moment later with the other four.[12]

Wing, under 250x magnification

The thorax is a shade of gray, sometimes even black, with four dark, longitudinal bands of even width on the dorsal surface. The whole body is covered with short hairs. Like other Diptera, houseflies have only one pair of wings; what would be the hind pair is reduced to small halteres that aid in flight stability. The wings are translucent with a yellowish tinge at their base. Characteristically, the medial vein (M1+2 or fourth long vein) shows a sharp upward bend. Each wing has a lobe at the back, the calypter, covering the haltere. The abdomen is gray or yellowish with a dark stripe and irregular dark markings at the side. It has 10 segments which bear spiracles for respiration. In males, the ninth segment bears a pair of claspers for copulation, and the 10th bears anal cerci in both sexes.[3][13]



Micrograph of tarsus of leg, showing claws and bristles including the central one between the two pulvilli known as the empodium

A variety of species around the world appear similar to the housefly, such as the lesser house fly, *Fannia canicularis*; the stable fly, *Stomoxys calcitrans*;[13] and other members of the genus *Musca* such as *M. vetustissima*, the Australian bush fly and several closely related taxa that include *M. primitiva*, *M. shanghaiensis*, *M. violacea*, and *M. varensis*.[14] The systematic identification of species may require the use of region-specific taxonomic keys and can require dissections of the male reproductive parts for confirmation.[15][16]

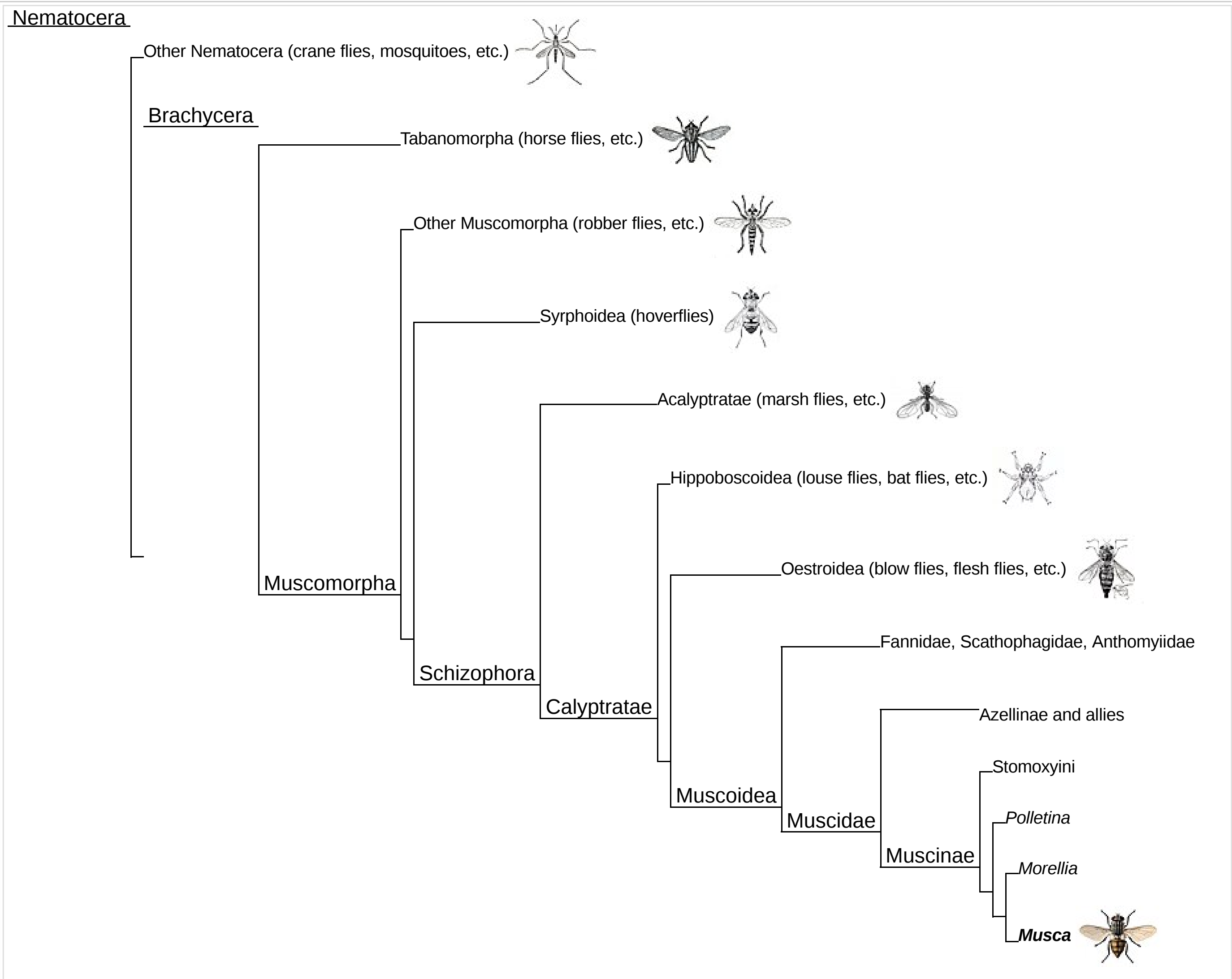
Distribution

The housefly is probably the insect with the widest distribution in the world; it is largely associated with humans and has accompanied them around the globe. It is present in the Arctic, as well as in the tropics, where it is abundant. It is present in all populated parts of Europe, Asia, Africa, Australasia, and the Americas.[3]

Evolution and taxonomy

Though the order of flies (Diptera) is much older, true houseflies are believed to have evolved in the beginning of the Cenozoic era.[17] The housefly's superfamily, Muscoidea, is most closely related to the Oestroidea (blow flies, flesh flies and allies), and more distantly to the Hippoboscoidea (louse flies, bat flies and allies). They are thought to have originated in the southern Palearctic region, particularly the Middle East. Because of their close, commensal relationship with humans, they probably owe their worldwide dispersal to co-migration with humans.[18]

The housefly was first described as *Musca domestica* in 1758 based on the common European specimens by the Swedish botanist and zoologist Carl Linnaeus in his *Systema naturae* and continues to be classified under that name.[19] A more detailed description was given in 1776 by the Danish entomologist Johan Christian Fabricius in his *Genera Insectorum*.[3]



Cladogram showing higher level classification[20][21][22] and position of *Musca* within the family Muscidae based on Couri and Carvalho 2003.[23]

Life cycle

Houseflies mating

Each female housefly can lay up to 500 eggs in her lifetime, in several batches of about 75 to 150. The eggs are white and are about 1.2 mm (0.05 in) in length, and they are deposited by the fly in a suitable place, usually dead and decaying organic matter, such as food waste, carrion, or faeces. Within a day, larvae (maggots) hatch from the eggs; they live and feed where they were laid. They are pale-whitish, 3 to 9 mm (0.12 to 0.35 in) long, thinner at the mouth end, and legless.[13] Larval development takes from two weeks, under optimal conditions, to 30 days or more in cooler conditions. The larvae avoid light; the interiors of heaps of animal manure provide nutrient-rich sites and ideal growing conditions, warm, moist, and dark.[13]

Larva and adult, by Amedeo John Engel Terzi (1872–1956)

At the end of their third instar, the larvae crawl to a dry, cool place and transform into pupae. The pupal case is cylindrical with rounded ends, about 1.2 mm (0.05 in) long, and formed from the last shed larval skin. It is yellowish at first, darkening through red and brown to nearly black as it ages. Pupae complete their development in two to six days at 35 °C (95 °F), but may take 20 days or more at 14 °C (57 °F).[13]

When metamorphosis is complete, the adult fly emerges from the pupa. To do this, it uses the ptilinum, an eversible pouch on its head, to tear open the end of the pupal case. The adult housefly lives from two weeks to a month in the wild, or longer in benign laboratory conditions. Having emerged from the pupa, it ceases to grow; a small fly is not necessarily a young fly, but is instead the result of getting insufficient food during the larval stage.[13]

Male houseflies are sexually mature after 16 hours and females after 24. Females produce a pheromone, (Z)-9-tricosene (muscalure). This cuticular hydrocarbon is not released into the air and males sense it only on contact with females;[12] it has found use as in pest control, for luring males to fly traps.[24][25] The male initiates the mating by bumping into the female, in the air or on the ground, known as a "strike". He climbs on to her thorax, and if she is receptive, a courtship period follows, in which the female vibrates her wings and the male strokes her head. The male then reverses onto her abdomen and the female pushes her ovipositor into his genital opening; copulation, with sperm transfer, lasts for several minutes. Females normally mate only once and then reject further advances from males, while males mate multiple times.[26] A volatile semiochemical that is deposited by females on their eggs attracts other gravid females and leads to clustered egg deposition.[27]

The larvae depend on warmth and sufficient moisture to develop; generally, the warmer the temperature, the faster they grow. In general, fresh swine and chicken manures present the best conditions for the developing larvae, reducing the larval period and increasing the size of the pupae. Cattle, goat, and horse manures produce fewer, smaller pupae, while fully composted swine manure, with a water content under 40%, produces none at all.[28] Pupae can range from about 8.0 to 20 milligrams (0.0003 to 0.0007 ounces) under different conditions.[29]

The lifecycle can be completed in seven to 10 days under optimal conditions, but may take up to two months in adverse circumstances. In temperate regions, 12 generations may occur per year, and in the tropics and subtropics, more than 20.[13]

Ecology

Housefly pupae killed by parasitoid wasp larvae: Each pupa has one hole through which a single adult wasp has emerged; the wasp larvae fed on the housefly larvae.

Houseflies play an important ecological role in breaking down and recycling organic matter. Adults are mainly carnivorous; their primary food is animal matter, carrion, and faeces, but they also consume milk, sugary substances, and rotting fruit and vegetables. Solid foods are softened with saliva before being sucked up.[7] They can be opportunistic blood feeders.[30] Houseflies have a mutualistic relationship with the bacterium *Klebsiella oxytoca*, which can live on the surface of housefly eggs and deter fungi which compete with the fly larvae for nutrients.[31]

Adult houseflies are diurnal and rest at night. If inside a building after dark, they tend to congregate on ceilings, beams, and overhead wires, while out of doors, they crawl into foliage or long grass, or rest in shrubs and trees or on wires.[13] In cooler climates, some houseflies hibernate in winter, choosing to do so in cracks and crevices, gaps in woodwork, and the folds of curtains. They arouse in the spring when the weather warms up, and search out a place to lay their eggs.[32]

Houseflies have many predators, including birds, reptiles, amphibians, various insects, and spiders. The eggs, larvae, and pupae have many species of stage-specific parasites and parasitoids. Some of the more important are the parasitic wasps *Muscidifurax uniraptor* and *Spalangia cameroni*; these lay their eggs in the fly larvae tissue and their offspring complete their development before the adult flies can emerge from the pupae.[13] Hister beetles feed on housefly larvae in manure heaps and the predatory mite *Macrocheles muscae domesticae* consumes housefly eggs, each mite eating 20 eggs per day.[33]

Houseflies sometimes carry phoretic (nonparasitic) passengers, including mites such as *Macrocheles muscaedomesticae*[34] and the pseudoscorpion *Lamprochernes chyzeri*.[35]

The pathogenic fungus *Entomophthora muscae* causes a fatal disease in houseflies. After infection, the fungal hyphae grow throughout the body, killing the fly in about five days. Infected flies have been known to seek high temperatures that could suppress the growth of the fungus. Affected females tend to be more attractive to males, but the fungus-host interactions have not been fully understood.[36] The housefly also acts as the alternative host to the parasitic nematode *Habronema muscae* that attacks horses.[37]

Relationship with humans

Flies are a nuisance, disturbing people at leisure and at work, but they are disliked principally because of their habits of contaminating foodstuffs. They alternate between breeding and feeding in dirty places with feeding on human foods, during which process they soften the food with saliva and deposit their feces, creating a health hazard.[38] However, fly larvae are as nutritious as fish meal, and could be used to convert waste to feed for fish and livestock.[39]


Housefly killed by the pathogenic fungus *Entomophthora muscae*

Flies have been used in art and artefacts in many cultures. In 16th- and 17th-century European vanitas paintings, flies sometimes occur as *memento mori*. They may also be used for other effects as in the Flemish painting, the *Master of Frankfurt* (1496). Fly amulets were popular in ancient Egypt.[40][41]

As a disease vector


Housefly lapping up food from a plate

Houseflies can fly for several miles from their breeding places,[42] carrying a wide variety of organisms on their hairs, mouthparts, vomitus, and faeces. Parasites carried include cysts of protozoa, e.g. *Entamoeba histolytica* and *Giardia lamblia* and eggs of helminths, e.g., *Ascaris lumbricoides*, *Trichuris trichiura*, *Hymenolepis nana*, and *Enterobius vermicularis*.[43] Houseflies do not serve as a secondary host or act as a reservoir of any bacteria of medical or veterinary importance, but they do serve as mechanical vectors to over 100 pathogens, such as those causing typhoid, cholera, salmonellosis,[44] bacillary dysentery,[45] tuberculosis, anthrax, ophthalmia,[46] and pyogenic cocci, making them especially problematic in hospitals and during outbreaks of certain diseases.[43] Disease-causing organisms on the outer surface of the fly may survive for a few hours, but those in the crop or gut can be viable for several days.[38] Usually, too few bacteria are on the external surface of the flies (except perhaps for *Shigella*) to cause infection, so the main routes to human infection are through the fly's regurgitation and defecation.[47]

In the early 20th century, Canadian public health workers believed that the control of flies was important in controlling the spread of tuberculosis. A "swat that fly" contest was held for children in Montreal in 1912.[48] Flies were targeted in 1916, when a polio epidemic broke out in the eastern United States. The belief that fly control was key to disease control continued, with extensive use of insecticidal spraying, well until the mid-1950s, declining only after the introduction of Salk's vaccine.[49] In China, Mao Zedong's Four Pests Campaign between 1958 and 1962 exhorted the people to catch and kill flies, along with rats, mosquitoes and sparrows.[50]

In warfare

During the Second World War, the Japanese worked on entomological warfare techniques under Shirō Ishii. Japanese Yagi bombs developed at Pingfan consisted of two compartments, one with houseflies and another with a bacterial slurry that coated the flies prior to release. *Vibrio cholerae*, which causes cholera, was the bacterium of choice, and was used in China in Baoshan in 1942, and in northern Shandong in 1943. Baoshan had been used by the Allies and bombing produced epidemics that killed 60,000 people in the initial stages reaching a radius of 200 km, which finally took a toll of 200,000 victims. The Shandong attack killed 210,000; the occupying Japanese troops had been vaccinated in advance.[51]

Philadelphia Department of Health poster warning the public of fly hazards (*c.* 1942)

In waste management

The ability of housefly larvae to feed and develop in a wide range of decaying organic matter is important for recycling of nutrients in nature. This could be exploited to combat ever-increasing amounts of waste.[52] Housefly larvae can be mass-reared in a controlled manner in animal manure, reducing the bulk of waste and minimizing environmental risks of its disposal.[53][54] Harvested maggots may be used as feed for animal nutrition.[54][55]

Control


Detail of a 1742 painting by Frans van der Mijn that uses a fly in a Renaissance allegory of touch theme

Flies can be controlled, at least to some extent, by physical, chemical, or biological means. Physical controls include screening with small mesh or the use of vertical strips of plastic or strings of beads in doorways to prevent entry of flies into buildings. Fans to create air movement or air barriers in doorways can deter flies from entering, and food premises often use fly-killing devices; sticky fly papers hanging from the ceiling are effective,[47] but electric "bug zappers" should not be used directly above food-handling areas because of scattering of contaminated insect parts.[56] Another approach is the elimination as far as possible of potential breeding sites. Keeping garbage in lidded containers and collecting it regularly and frequently, prevents any eggs laid from developing into adults. Unhygienic rubbish tips are a prime fly-breeding site, but if garbage is covered by a layer of soil, preferably daily, this can be avoided.[47]

Insecticides can be used. Larvicides kill the developing larvae, but large quantities may need to be used to reach areas below the surface. Aerosols can be used in buildings to "zap" flies, but outside applications are only temporarily effective. Residual sprays on walls or resting sites have a longer-lasting effect.[47] Many strains of housefly have become immune to the most commonly used insecticides.[57][58]

Several means of biological pest control have been investigated. These include the introduction of another species, the black soldier fly (*Hermetia illucens*), whose larvae compete with those of the housefly for resources.[59] The introduction of dung beetles to churn up the surface of a manure heap and render it unsuitable for breeding is another approach.[59] Augmentative biological control by releasing parasitoids can be used, but flies breed so fast that the natural enemies are unable to keep up.[60]

In science

The ease of culturing houseflies, and the relative ease of handling them when compared to the fruit fly *Drosophila*, have made them useful as model organism for use in laboratories. The American entomologist Vincent Dethier, in his humorous *To Know A Fly* (1962), pointed out that as a laboratory animal, houseflies did not trouble anyone sensitive to animal cruelty. Houseflies have a small number of chromosomes, haploid six or diploid 12.[61] Because the somatic tissue of the housefly consists of long-lived postmitotic cells, it can be used as an informative model system for understanding cumulative age-related cellular alterations. Oxidative DNA damage 8-hydroxydeoxyguanosine in houseflies was found in one study to increase with age and reduce life expectancy supporting the hypothesis that oxidative molecular damage is a causal factor in senescence (aging).[62][63][64]

The housefly is an object of biological research, partly for its variable sex-determination mechanism. Although a wide variety of sex-determination mechanisms exists in nature (e.g. male and female heterogamy, haplodiploidy, environmental factors), the way sex is determined is usually fixed within a species. The housefly is, however, thought to exhibit multiple mechanisms for sex determination, such as male heterogamy (like most insects and mammals), female heterogamy (like birds), and maternal control over offspring sex. This is because a male-determining gene (*Mdmd*) can be found on most or all housefly chromosomes.[65] Sexual differentiation is controlled as in other insects by an ancient developmental switch, doublesex, which is regulated by the transformer protein in many different insects.[66] *Mdmd* causes male development by negatively regulating *transformer*. There is also a female-determining allele of *transformer* that is not sensitive to the negative regulation of *Mdmd*.[67]

William Blake's illustration of "The Fly" in *Songs of Innocence and of Experience*, 1794

The antimicrobial peptides produced by housefly maggots are of pharmacological interest.[68]

In the 1970s, the aircraft modeller Frank Ehling constructed miniature balsa-wood aircraft powered by live houseflies.[69] Studies of tethered flies have helped in the understanding of insect vision, sensory perception, and flight control.[70]

In literature

The Impertinent Insect is a group of five fables, sometimes ascribed to Aesop, concerning an insect, in one version a fly, which puffs itself up to seem important. In the Biblical fourth plague of Egypt, flies represent death and decay, while the Philistine god Beelzebub's name may mean "lord of the flies".[71] In Greek mythology, Myiagros was a god who chased away flies during the sacrifices to Zeus and Athena; Zeus sent a fly to bite Pegasus, causing Bellerophon to fall back to Earth when he attempted to ride the winged steed to Mount Olympus.[72] In the traditional Navajo religion, Big Fly is an important spirit being.[73][74][75]

William Blake's 1794 poem "The Fly", part of his collection *Songs of Experience*, deals with the insect's mortality, subject to uncontrollable circumstances, just like humans.[76] Emily Dickinson's 1855 poem "I Heard a Fly Buzz When I Died" speaks of flies in the context of death.[77] In William Golding's 1954 novel *Lord of the Flies*, the fly is however a symbol of the children involved.[78]

Ogden Nash's humorous two-line 1942 poem "God in His wisdom made the fly/And then forgot to tell us why." indicates the debate about the value of biodiversity, given that even those considered by humans as pests have their place in the world's ecosystems.[79]

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Cricket (insect)

Crickets (also known as "**true crickets**"), of the family **Gryllidae**, are insects related to bush crickets, and, more distantly, to grasshoppers. The Gryllidae have mainly cylindrical bodies, round heads, and long antennae. Behind the head is a smooth, robust pronotum. The abdomen ends in a pair of long cerci; females have a long, cylindrical ovipositor. The hind legs have enlarged femora, providing power for jumping. The front wings are adapted as tough, leathery elytra, and some crickets chirp by rubbing parts of these together. The hind wings are membranous and folded when not in use for flight; many species, however, are flightless. The largest members of the family are the bull crickets, *Brachytrupes*, which are up to 5 cm (2 in) long.

More than 900 species of crickets are described; the Gryllidae are distributed all around the world except at latitudes 55° or higher, with the greatest diversity being in the tropics. They occur in varied habitats from grassland, bushes, and forests to marshes, beaches, and caves. Crickets are mainly nocturnal, and are best known for the loud, persistent, chirping song of males trying to attract females, although some species are mute. The singing species have good hearing, via the tympana on the tibiae of the front legs.

Crickets often appear as characters in literature. The Talking Cricket features in Carlo Collodi's 1883 children's book, *The Adventures of Pinocchio*, and in films based on the book. The eponymous insect is central to Charles Dickens's 1845 *The Cricket on the Hearth*, as is the chirping insect in George Selden's 1960 *The Cricket in Times Square*. Crickets are celebrated in poems by William Wordsworth, John Keats, and Du Fu. They are kept as pets in countries from China to Europe, sometimes for cricket fighting. Crickets are efficient at converting their food into body mass, making them a candidate for food production. They are used as human food in Southeast Asia, where they are sold deep-fried in markets as snacks. They are also used to feed carnivorous pets and zoo animals. In Brazilian folklore, crickets feature as omens of various events.

Cricket

Temporal range: Triassic–Recent

PreЄ Є O S D C P T J K PgN

[1]

Juvenile *Gryllus campestris*

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Ensifera
Superfamily:	Grylloidea
Family:	Gryllidae Laicharting, 1781[2]

Subfamilies

See Taxonomy section

Synonyms[2]

- *Gryllides* Laicharting, 1781

Contents

- *Paragryllidae* Desutter-Grandcolas, 1987

Description


African field cricket *Gryllus bimaculatus*

Crickets are small to medium-sized insects with mostly cylindrical, somewhat vertically flattened bodies. The head is spherical with long slender antennae arising from cone-shaped scapes (first segments) and just behind these are two large compound eyes. On the forehead are three ocelli (simple eyes). The pronotum (first thoracic segment) is trapezoidal in shape, robust, and well-sclerotinized. It is smooth and has neither dorsal or lateral keels (ridges).[3]

At the tip of the abdomen is a pair of long cerci (paired appendages on rearmost segment), and in females, the ovipositor is cylindrical, long and narrow, smooth and shiny. The femora (third segments) of the back pair of legs are greatly enlarged for jumping. The tibiae (fourth segments) of the hind legs are armed with a number of moveable spurs, the arrangement of which is characteristic of each species. The tibiae of the front legs bear one or more tympani which are used for the reception of sound.[3]

The wings lie flat on the body and are very variable in size between species, being reduced in size in some crickets and missing in others. The fore wings are elytra made of tough chitin, acting as a protective shield for the soft parts of the body and in males, bear the stridulatory organs for the production of sound. The hind pair is membranous, folding fan-wise under the fore wings. In many species, the wings are not adapted for flight.[1]

The largest members of the family are the 5 cm (2 in)-long bull crickets (*Brachytrupes*) which excavate burrows a metre or more deep. The tree crickets (Oecanthinae) are delicate white or pale green insects with transparent fore wings, while the field crickets (Gryllinae) are robust brown or black insects.[1]

Distribution and habitat

Crickets have a cosmopolitan distribution, being found in all parts of the world with the exception of cold regions at latitudes higher than about 55° North and South. They have colonised many large and small islands, sometimes flying over the sea to reach these locations, or perhaps conveyed on floating timber or by human activity. The greatest diversity occurs in tropical locations,

such as in Malaysia, where 88 species were heard chirping from a single location near Kuala Lumpur. A greater number than this could have been present because some species are mute.[1]

Crickets are found in many habitats. Members of several subfamilies are found in the upper tree canopy, in bushes, and among grasses and herbs. They also occur on the ground and in caves, and some are subterranean, excavating shallow or deep burrows. Some make home in rotting wood, and certain beach-dwelling species can run and jump over the surface of water.[1]

Biology

Defence

Crickets are relatively defenceless, soft-bodied insects. Most species are nocturnal and spend the day hidden in cracks, under bark, inside curling leaves, under stones or fallen logs, in leaf litter, or in the cracks in the ground that develop in dry weather. Some excavate their own shallow holes in rotting wood or underground and fold in their antennae to conceal their presence. Some of these burrows are temporary shelters, used for a single day, but others serve as more permanent residences and places for mating and laying eggs. Crickets burrow by loosening the soil with the mandibles and then carrying it with the limbs, flicking it backwards with the hind legs or pushing it with the head.[4]

Other defensive strategies are the use of camouflage, fleeing, and aggression. Some species have adopted colourings, shapes, and patterns that make it difficult for predators that hunt by sight to detect them. They tend to be dull shades of brown, grey, and green that blend into their background, and desert species tend to be pale. Some species can fly, but the mode of flight tends to be clumsy, so the most usual response to danger is to scuttle away to find a hiding place.[4]

Chirping

Most male crickets make a loud chirping sound by stridulation (scraping two specially textured limbs together). The stridulatory organ is located on the tegmen, or fore wing, which is leathery in texture. A large vein runs along the centre of each tegmen, with comb-like serrations on its edge forming a file-like structure, and at the rear edge of the tegmen is a scraper. The tegmina are held at an angle to the body and rhythmically raised and lowered which causes the scraper on one wing to rasp on the file on the other. The central part of the tegmen contains the "harp", an area of thick, sclerotinized membrane which resonates and amplifies the volume of sound, as does the pocket of air between the tegmina and the body wall. Most female crickets lack the necessary adaptations to stridulate, so make no sound.[5]

A male *Gryllus* cricket chirping: Its head faces its burrow; the leathery fore wings (tegmina; singular "tegmen") are raised (clear of the more delicate hind wings) and are being scraped against each other (stridulation) to produce the song. The burrow acts as a resonator, amplifying the sound.

Several types of cricket songs are in the repertoire of some species. The calling song attracts females and repels other males, and is fairly loud. The courting song is used when a female cricket is near and encourages her to mate with the caller. A triumphal song is produced for a brief period after a successful mating, and may reinforce the mating bond to encourage the female to lay some eggs rather than find another male.[6] An aggressive song is triggered by contact chemoreceptors on the antennae that detect the presence of another male cricket.[7]

Crickets chirp at different rates depending on their species and the temperature of their environment. Most species chirp at higher rates the higher the temperature is (about 62 chirps a minute at 13 °C (55 °F) in one common species; each species has its own rate). The relationship between temperature and the rate of chirping is known as Dolbear's law. According to this law, counting

the number of chirps produced in 14 seconds by the snowy tree cricket, common in the United States, and adding 40 will approximate the temperature in degrees Fahrenheit.[6]

In 1975, Dr. William H. Cade discovered that the parasitic tachinid fly *Ormia ochracea* is attracted to the song of the cricket, and uses it to locate the male to deposit her larvae on him. It was the first known example of a natural enemy that locates its host or prey using the mating signal.[8] Since then, many species of crickets have been found to be carrying the same parasitic fly, or related species. In response to this selective pressure, a mutation leaving males unable to chirp was observed amongst a population of *Teleogryllus oceanicus* on the Hawaiian island of Kauai, enabling these crickets to elude their parasitoid predators.[9] A different mutation with the same effect was also discovered on the neighboring island of Oahu (ca. 100 miles (160 km) away).[10] Recently, new "purring" males of the same species in Hawaii are able to produce a novel auditory sexual signal that can be used to attract females while greatly reducing the likelihood of parasitoid attack from the fly.[11]

0:00 / 0:00

The calling song of a field cricket

Flight

Some species, such as the ground crickets (Nemobiinae), are wingless; others have small fore wings and no hind wings (*Copholandrevus*), others lack hind wings and have shortened fore wings in females only, while others are macropterous, with the hind wings longer than the fore wings. In *Teleogryllus*, the proportion of macropterous individuals varies from very low to 100%. Probably, most species with hind wings longer than fore wings engage in flight.[3]

Some species, such as *Gryllus assimilis*, take off, fly, and land efficiently and well, while other species are clumsy fliers.[1] In some species, the hind wings are shed, leaving wing stumps, usually after dispersal of the insect by flight. In other species, they may be pulled off and consumed by the cricket itself or by another individual, probably providing a nutritional boost.[12]

Gryllus firmus exhibits wing polymorphism; some individuals have fully functional, long hind wings and others have short wings and cannot fly. The short-winged females have smaller flight muscles, greater ovarian development, and produce more eggs, so the polymorphism adapts the cricket for either dispersal or reproduction. In some long-winged individuals, the flight muscles deteriorate during adulthood and the insect's reproductive capabilities improve.[13]

Diet

Captive crickets are omnivorous; when deprived of their natural diet, they accept a wide range of organic foodstuffs. Some species are completely herbivorous, feeding on flowers, fruit, and leaves, with ground-based species consuming seedlings, grasses, pieces of leaf, and the shoots of young plants. Others are more predatory and include in their diet invertebrate eggs, larvae, pupae, moulting insects, scale insects, and aphids.[14] Many are scavengers and consume various organic remains, decaying plants, seedlings, and fungi.[15] In captivity, many species have been successfully reared on a diet of ground, commercial dry dog food, supplemented with lettuce and aphids.[14]

Two adult domestic crickets, *Acheta domestica*, feeding on carrot

Crickets have relatively powerful jaws, and several species have been known to bite humans.[16]

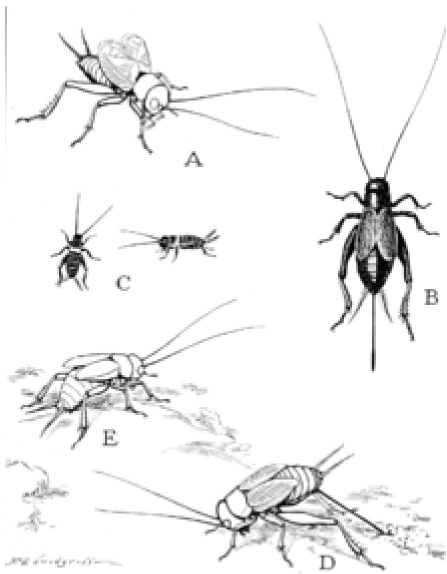
Reproduction and lifecycle

Male crickets establish their dominance over each other by aggression. They start by lashing each other with their antennae and flaring their mandibles. Unless one retreats at this stage, they resort to grappling, at the same time each emitting calls that are quite unlike those uttered in other circumstances. When one achieves dominance, it sings loudly, while the loser remains silent.[17]

Females are generally attracted to males by their calls, though in nonstridulatory species, some other mechanism must be involved. After the pair has made antennal contact, a courtship period may occur during which the character of the call changes. The female mounts the male and a single spermatophore is transferred to the external genitalia of the female. Sperm flows from this into the female's oviduct over a period of a few minutes or up to an hour, depending on species. After copulation, the female may remove or eat the spermatophore; males may attempt to prevent this with various ritualised behaviours. The female may mate on several occasions with different males.[18]

Most crickets lay their eggs in the soil or inside the stems of plants, and to do this, female crickets have a long, needle-like or sabre-like egg-laying organ called an ovipositor. Some ground-dwelling species have dispensed with this, either depositing their eggs in an underground chamber or pushing them into the wall of a burrow.[1] The short-tailed cricket (*Anurogryllus*) excavates a burrow with chambers and a defecating area, lays its eggs in a pile on a chamber floor, and after the eggs have hatched, feeds the juveniles for about a month.[19]

Crickets are hemimetabolic insects, whose lifecycle consists of an egg stage, a larval or nymph stage that increasingly resembles the adult form as the nymph grows, and an adult stage. The egg hatches into a nymph about the size of a fruit fly. This passes through about 10 larval stages, and with each successive moult, it becomes more like an adult. After the final moult, the genitalia and wings are fully developed, but a period of maturation is needed before the cricket is ready to breed.[20]



Various instars of *Gryllus assimilis*, by Robert Evans Snodgrass, 1930

Inbreeding avoidance

Some species of cricket are polyandrous. In *Gryllus bimaculatus,* the females select and mate with multiple viable sperm donors, preferring novel mates.[21] Female *Teleogryllus oceanicus* crickets from natural populations similarly mate and store sperm from multiple males.[22] Female crickets exert a postcopulatory fertilization bias in favour of unrelated males to avoid the genetic consequences of inbreeding. Fertilization bias depends on the control of sperm transport to the sperm storage organs. The inhibition of sperm storage by female crickets can act as a form of cryptic female choice to avoid the severe negative effects of inbreeding.[23] Controlled-breeding experiments with the cricket *Gryllus firmus* demonstrated inbreeding depression, as nymphal weight and early fecundity declined substantially over the generations'[24] this was caused as expected by an increased frequency of homozygous combinations of deleterious recessive alleles.[24][25]

Predators, parasites, and pathogens

Crickets have many natural enemies and are subject to various pathogens and parasites. They are eaten by large numbers of vertebrate and invertebrate predators and their hard parts are often found during the examination of animal intestines.[4] Mediterranean house geckos (*Hemidactylus turcicus*) have learned that although a calling decorated cricket (*Gryllodes supplicans*) may be safely positioned in an out-of-reach burrow, female crickets attracted to the call can be intercepted and eaten.[17]

Crickets are reared as food for pets and zoo animals like this baboon spider, *Pterinochilus murinus*, emerging from its den to feed.

The entomopathogenic fungus *Metarhizium anisopliae* attacks and kills crickets and has been used as the basis of control in pest populations.[4] The insects are also affected by the cricket paralysis virus, which has caused high levels of fatalities in cricket-rearing facilities.[26] Other fatal diseases that have been identified in mass-rearing establishments include *Rickettsia* and three further viruses. The diseases may spread more rapidly if the crickets become cannibalistic and eat the corpses.[4]

Red parasitic mites sometimes attach themselves to the dorsal region of crickets and may greatly affect them.[4] The horsehair worm *Paragordius varius* is an internal parasite and can control the behaviour of its cricket host and cause it to enter water, where the parasite continues its lifecycle and the cricket likely drowns.[27] The larvae of the sarcophagid fly *Sarcophaga kellyi* develop inside the body cavity of field crickets.[28] Female parasitic wasps of *Rhopalosoma* lay their eggs on crickets, and their developing larvae gradually devour their hosts. Other wasps in the family Scelionidae are egg parasitoids, seeking out batches of eggs laid by crickets in plant tissues in which to insert their eggs.[4]

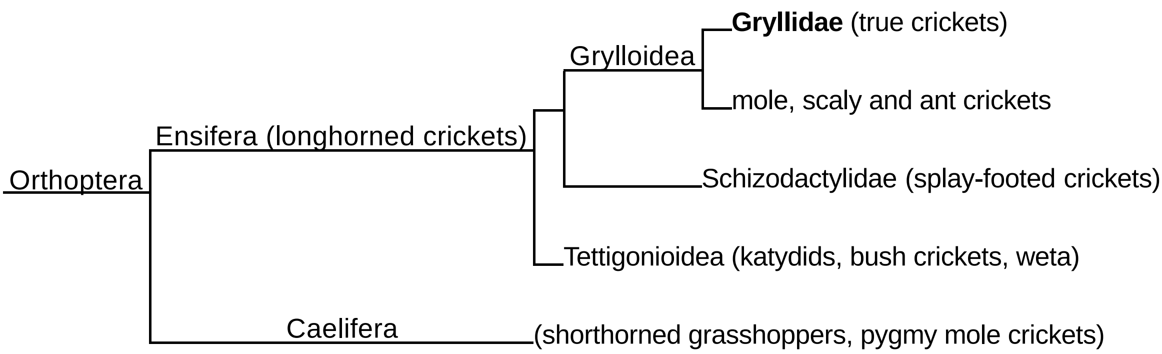
The fly *Ormia ochracea* has very acute hearing and targets calling male crickets. It locates its prey by ear and then lays its eggs nearby. The developing larvae burrow inside any crickets with which they come in contact and in the course of a week or so, devour what remains of the host before pupating.[29] In Florida, the parasitic flies were only present in the autumn, and at that time of year, the males sang less but for longer periods. A trade-off exists for the male between attracting females and being parasitized.[30]

Phylogeny and taxonomy

The phylogenetic relationships of the Gryllidae, summarized by Darryl Gwynne in 1995 from his own work (using mainly anatomical characteristics) and that of earlier authors,[a] are shown in the following cladogram, with the Orthoptera divided into two main groups, Ensifera (crickets *sensu lato*) and Caelifera (grasshoppers). Fossil Ensifera are found from the late Carboniferous period (300 Mya) onwards,[31][32] and the true crickets, Gryllidae, from the Triassic period (250 to 200 Mya).[1]

Cladogram after Gwynne, 1995:[31]

Fossil cricket from the Cretaceous of Brazil



A phylogenetic study by Jost & Shaw in 2006 using sequences from 18S, 28S, and 16S rRNA supported the monophyly of Ensifera. Most ensiferan families were also found to be monophyletic, and the superfamily Gryllacridoidea was found to include Stenopelmatidae, Anostostomatidae, Gryllacrididae and Lezina. Schizodactylidae and Grylloidea were shown to be sister taxa, and Rhaphidophoridae and Tettigoniidae were found to be more closely related to Grylloidea than had previously been thought. The authors stated that "a high degree of conflict exists between the molecular and morphological data, possibly indicating that much homoplasy is present in Ensifera, particularly in acoustic structures." They considered that tegmen stridulation and tibial tympanae are ancestral to Ensifera and have been lost on multiple occasions, especially within the Gryllidae.[33]

Subfamilies

More than 900 species of Gryllidae (true crickets) are known.[34][b] The family is divided into these subfamily groups, subfamilies, and extinct genera (not placed within the subfamilies):[35]

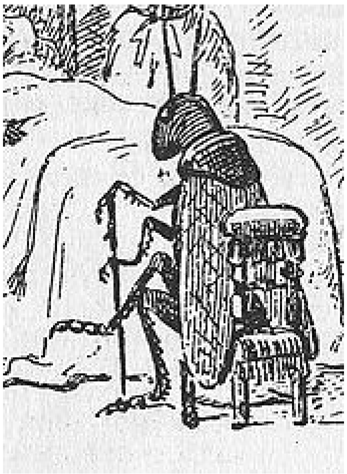
- Subfamily group Gryllinae Laicharting, 1781 – common or field crickets
  - Gryllinae Laicharting, 1781
  - Gryllomiminae Gorochov, 1986
  - Gryllomorphinae Saussure, 1877
  - Gryllospeculinae † Gorochov, 1985
  - Itarinae Shiraki, 1930
  - Landrevinae Gorochov, 1982
  - Sclerogryllinae Gorochov, 1985
- Subfamily group Podoscirtinae
  - Euscyrtinae Gorochov, 1985
  - Hapithinae Gorochov, 1986
  - Pentacentrinae Saussure, 1878
  - Podoscirtinae Saussure, 1878 – anomalous crickets
- Subfamily group Phalangopsinae
  - Cachoplistinae Saussure, 1877
  - Paragryllinae Desutter-Grandcolas, 1987
  - Phalangopsinae Blanchard, 1845 – spider crickets
  - Phaloriinae Gorochov, 1985
  - Pteroplistinae Chopard, 1936
- Subfamily Eneopterinae Saussure, 1893 – bush crickets (American usage), not to be confused with the Tettigoniidae (katydids or bush crickets)
- Subfamily Oecanthinae Blanchard, 1845 – tree crickets
- Subfamily unplaced: extinct
  - Genus *Gryllidium* † Westwood, 1854
  - Genus *Liaonemobius* † Ren, 1998
  - Genus *Lithogryllites* † Cockerell, 1908
  - Genus *Menonia* † George, 1936
  - Genus *Nanaripegryllus* † Martins-Neto, 2002

In human culture

Folklore and myth

The folklore and mythology surrounding crickets is extensive.[36] The singing of crickets in the folklore of Brazil and elsewhere is sometimes taken to be a sign of impending rain, or of a financial windfall. In Álvar Núñez Cabeza de Vaca's chronicles of the Spanish conquest of the Americas, the sudden chirping of a cricket heralded the sighting of land for his crew, just as their water supply had run out.[37] In Caraguatatuba, Brazil, a black cricket in a room is said to portend illness; a gray one, money; and a

green one, hope.[37] In Alagoas state, northeast Brazil, a cricket announces death, thus it is killed if it chirps in a house.[38] In Barbados, a loud cricket means money is coming in; hence, a cricket must not be killed or evicted if it chirps inside a house. However, another type of cricket that is less noisy forebodes illness or death.[39]



Il Grillo Parlante (The Talking Cricket) illustrated by Enrico Mazzanti for Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*)

Illustration for Charles Dickens's 1883 *Cricket on the Hearth* by Fred Barnard

In literature

Crickets feature as major characters in novels and children's books. Charles Dickens's 1845 novella *The Cricket on the Hearth*, divided into sections called "Chirps", tells the story of a cricket which chirps on the hearth and acts as a guardian angel to a family.[40] Carlo Collodi's 1883 children's book "Le avventure di Pinocchio" (*The Adventures of Pinocchio*) featured "Il Grillo Parlante" (The Talking Cricket) as one of its characters.[41] George Selden's 1960 children's book *The Cricket in Times Square* tells the story of Chester the cricket from Connecticut who joins a family and their other animals, and is taken to see Times Square in New York.[42] The story, which won the Newbery Honor,[43] came to Selden on hearing a real cricket chirp in Times Square.[44]

Souvenirs entomologiques, a book written by the French entomologist Jean-Henri Fabre, devotes a whole chapter to the cricket, discussing its construction of a burrow and its song-making. The account is mainly of the field cricket, but also mentions the Italian cricket.[45]

Crickets have from time to time appeared in poetry. William Wordsworth's 1805 poem *The Cottager to Her Infant* includes the couplet "The kitten sleeps upon the hearth, The crickets long have ceased their mirth".[46] John Keats's 1819 poem *Ode to Autumn* includes the lines "Hedge-crickets sing; and now with treble soft / The redbreast whistles from a garden-croft".[47] The Chinese Tang dynasty poet Du Fu (712–770) wrote a poem that in the translation by J. P. Seaton begins "House cricket ... Trifling thing. And yet how his mournful song moves us. Out in the grass his cry was a tremble, But now, he trills beneath our bed, to share his sorrow."[48]

As pets and fighting animals

Crickets are kept as pets and are considered good luck in some countries; in China, they are sometimes kept in cages or in hollowed-out gourds specially created in novel shapes.[49] The practice was common in Japan for thousands of years; it peaked in the 19th century, though crickets are still sold at pet shops.[50] It is also common to have them as caged pets in some European countries, particularly in the Iberian Peninsula. Cricket fighting is a traditional Chinese pastime that dates back to the Tang dynasty (618–907). Originally an indulgence of emperors, cricket fighting later became popular among commoners.[51] The dominance and fighting ability of males does not depend on strength alone; it has been found that they become more aggressive after certain pre-fight

Meiji period cricket holder in the form of a *norimono* palanquin, c. 1850

experiences such as isolation, or when defending a refuge. Crickets forced to fly for a short while will afterwards fight for two to three times longer than they otherwise would.[52]

As food

Deep-fried house crickets (*Acheta domesticus*) at a market in Thailand

In the southern part of Asia including Cambodia, Laos, Thailand, and Vietnam, crickets are commonly eaten as a snack, prepared by deep frying the soaked and cleaned insects.[53] In Thailand, there are 20,000 farmers rearing crickets, with an estimated production of 7,500 tons per year[54] and United Nation's FAO has implemented a project in Laos to improve cricket farming and consequently food security.[55] The food conversion efficiency of house crickets (*Acheta domesticus*) is 1.7, some five times higher than that for beef cattle, and if their fecundity is taken into account, 15 to 20 times higher.[56][57]

A cricket flour energy bar with the equivalent of approximately 40 crickets in each bar.

Cricket flour can be used as an additive to consumer foods such as pasta, bread, crackers, and cookies. The cricket flour is being used in protein bars, pet foods, livestock feed, nutraceuticals, and other industrial uses. The United Nations says the use of insect protein, such as cricket flour, could be critical in feeding the growing population of the planet while being less damaging to the environment.[58]

Crickets are also reared as food for carnivorous zoo animals, laboratory animals, and pets.[4][59] They may be "gut loaded" with additional minerals, such as calcium, to provide a balanced diet for predators such as tree frogs (Hylidae).[60]

Common expressions

By the 19th century "cricket" and "crickets" were in use as euphemisms for using Christ as an interjection. The addition of "Jiminy" (a variation of "Gemini"), sometimes shortened to "Jimmy" created the expressions "Jiminy Cricket!" or "Jimmy Crickets!" as less blasphemous alternatives to exclaiming "Jesus Christ!"[61]

By the end of the 20th century the sound of chirping crickets came to represent quietude in literature, theatre and film. From this sentiment arose expressions equating "crickets" with silence altogether, particularly when a group of assembled people makes no noise. These expressions have grown from the more descriptive, "so quiet that you can hear crickets," to simply saying , "crickets" as shorthand for "complete silence."[62]

In popular culture

Cricket characters feature in the Walt Disney animated movies *Pinocchio* (1940), where Jiminy Cricket becomes the title character's conscience, and in *Mulan* (1998), where Cri-kee is carried in a cage as a symbol of luck, in the Asian manner. The Crickets was the name of Buddy Holly's rock and roll band;[63] Holly's home town baseball team in the 1990s was called the Lubbock Crickets.[64] *Cricket* is the name of a US children's literary magazine founded in 1973; it uses a cast of insect characters.[65] The sound of crickets is often used in media to emphasize silence, often for comic effect after an awkward joke, in a similar manner to tumbleweed.[66]

Notes

Jiminy Cricket, from Walt Disney's movie *Pinocchio* (1940)

a. Gwynne cites Ander 1939, Zeuner 1939, Judd 1947, Key 1970, Ragge 1977 and Rentz 1991 as supporting the two-part scheme (Ensifera, Caelifera) in his 1995 paper.[31]

b. Some groups in the Ensifera may be called crickets *sensu lato*, including the Rhaphidophoridae – cave or camel crickets; Stenopelmatidae – Jerusalem or sand crickets; Mogoplistidae – scaly crickets; Gryllotalpidae – mole crickets; Anabrus – mormon crickets; Myrmecophilidae – ant crickets; and Tettigoniidae – katydids or bush crickets.

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Beetle

Beetles are a group of insects that form the order **Coleoptera**, in the superorder Endopterygota. Their front pair of wings are hardened into wing-cases, elytra, distinguishing them from most other insects. The Coleoptera, with about 400,000 species, is the largest of all orders, constituting almost 40% of described insects and 25% of all known animal life-forms; new species are discovered frequently. The largest of all families, the Curculionidae (weevils), with some 83,000 member species, belongs to this order. Found in almost every habitat except the sea and the polar regions, they interact with their ecosystems in several ways: beetles often feed on plants and fungi, break down animal and plant debris, and eat other invertebrates. Some species are serious agricultural pests, such as the Colorado potato beetle, while others such as Coccinellidae (ladybirds or ladybugs) eat aphids, scale insects, thrips, and other plant-sucking insects that damage crops.

Beetles typically have a particularly hard exoskeleton including the elytra, though some such as the rove beetles have very short elytra while blister beetles have softer elytra. The general anatomy of a beetle is quite uniform and typical of insects, although there are several examples of novelty, such as adaptations in water beetles which trap air bubbles under the elytra for use while diving. Beetles are endopterygotes, which means that they undergo complete metamorphosis, with a series of conspicuous and relatively abrupt changes in body structure between hatching and becoming adult after a relatively immobile pupal stage. Some, such as stag beetles, have a marked sexual dimorphism, the males possessing enormously enlarged mandibles which they use to fight other males. Many beetles are aposematic, with bright colours and patterns warning of their toxicity, while others are harmless Batesian mimics of such insects. Many beetles, including those that live in sandy places, have effective camouflage.

Beetles are prominent in human culture, from the sacred scarabs of ancient Egypt to beetlewing art and use as pets or fighting insects for entertainment and gambling. Many beetle groups are brightly and attractively coloured making them objects of collection and decorative displays. Over 300 species are used as food, mostly as larvae; species widely consumed include mealworms and rhinoceros beetle larvae. However, the major impact of beetles on human life is as agricultural, forestry, and horticultural pests. Serious pests include the boll weevil of cotton, the Colorado potato beetle, the coconut hispine beetle, and the mountain pine beetle. Most beetles, however, do not cause economic damage and many, such as the lady beetles and dung beetles are beneficial by helping to control insect pests.

Beetle

Temporal range: 318–0 Ma

PreЄ Є O S D C P T J K PgN

Late Carboniferous–Holocene

Clockwise from top left: female golden stag beetle (*Lamprima aurata*), rhinoceros beetle (*Megasoma* sp.), long nose weevil (*Rhinotia hemistictus*), cowboy beetle (*Chondropyga dorsalis*), and a species of *Amblytelus*.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
(unranked):	Endopterygota
Order:	Coleoptera Linnaeus, 1758

Suborders

- Adephaga
- Archostemata
- Myxophaga
- Polyphaga
- †Protocoleoptera[1]

See subgroups of the order Coleoptera

Contents

Etymology

The name of the taxonomic order, Coleoptera, comes from the Greek *koleopteros* (κολεόπτερος), given to the group by Aristotle for their elytra, hardened shield-like forewings, from *koleos*, sheath, and *pteron*, wing. The English name beetle comes from the Old English word *bitela*, little biter, related to *bītan* (to bite),[2][3] leading to Middle English *betylle*.[4] Another Old English name for beetle is *ċeafor*, chafer, used in names such as cockchafer, from the Proto-Germanic **kebrô* ("beetle"; compare German *Käfer*, Dutch *kever*).[5]

Coleoptera at the Staatliches Museum für Naturkunde Karlsruhe, Germany

Distribution and diversity

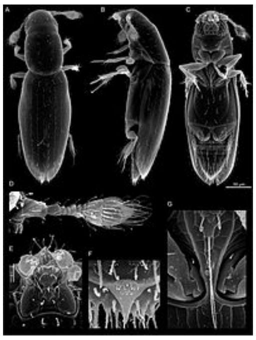
Beetles are by far the largest order of insects: the roughly 400,000 species make up about 40% of all insect species so far described, and about 25% of all animals.[1][6][7][8][9][10] A 2015 study provided four independent estimates of the total number of beetle species, giving a mean estimate of some 1.5 million with a "surprisingly narrow range"[11] spanning all four estimates from a minimum of 0.9 to a maximum of 2.1 million beetle species. The four estimates made use of host-specificity relationships (1.5 to 1.9 million), ratios with other taxa (0.9 to 1.2 million), plant:beetle ratios (1.2 to 1.3), and extrapolations based on body size by year of description (1.7 to 2.1 million).[11][12]

Beetles are found in nearly all habitats, including freshwater and coastal habitats, wherever vegetative foliage is found, from trees and their bark to flowers, leaves, and underground near roots - even inside plants in galls, in every plant tissue, including dead or decaying ones.[13] Tropical forest canopies have a large and diverse fauna of beetles,[14] including Carabidae,[15] Chrysomelidae,[16] and Scarabaeidae.[17]

The heaviest beetle, indeed the heaviest insect stage, is the larva of the goliath beetle, *Goliathus goliatus*, which can attain a mass of at least 115 g (4.1 oz) and a length of 11.5 cm (4.5 in). Adult male goliath beetles are the heaviest beetle in its adult stage, weighing 70–100 g (2.5–3.5 oz) and measuring up to 11 cm (4.3 in).[18] Adult elephant beetles, *Megasoma elephas* and *Megasoma actaeon* often reach 50 g (1.8 oz) and 10 cm (3.9 in).[19]

The longest beetle is the Hercules beetle *Dynastes hercules*, with a maximum overall length of at least 16.7 cm (6.6 in) including the very long pronotal horn. The smallest recorded beetle and the smallest free-living insect (as of 2015), is the featherwing beetle *Scydosella musawasensis* which may measure as little as 325 μm in length.[20]

Titan beetle, *Titanus giganteus*, a tropical longhorn, is one of the largest and heaviest insects in the world.



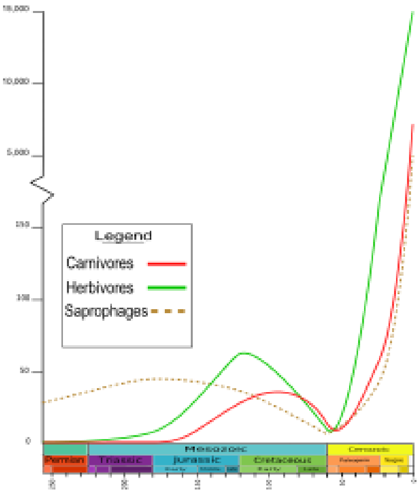
Scydosella musawasensis, the smallest known beetle: scale bar (right) is 50 μm.

Hercules beetle, *Dynastes hercules ecuatorianus*, the longest of all beetles

Evolution

Late Paleozoic

The oldest known fossil insect that unequivocally resembles a Coleopteran is from the Lower Permian Period about 270 million years ago (mya), though these members of the family Tshekardocoleidae have 13-segmented antennae, elytra with more fully developed venation and more irregular longitudinal ribbing, and abdomen and ovipositor extending beyond the apex of the elytra. In the Permian–Triassic extinction event at the end of the Permian, some 30% of all insect species became extinct, so the fossil record of insects only includes beetles from the Lower Triassic 220 mya. Around this time, during the Late Triassic, fungus-feeding species such as Cupedidae appear in the fossil record. In the stages of the Upper Triassic, alga-feeding insects such as Triaplidae and Hydrophilidae begin to appear, alongside predatory water beetles. The first weevils, including the Obrienidae, appear alongside the first rove beetles (Staphylinidae), which closely resemble recent species.[21] Some entomologists are sceptical that such early insects are so closely related to present-day species, arguing that this is extremely unlikely; for example, the structure of the metepisternum suggests that the Obrienidae could be Archostemata, not weevils at all, despite fossils with weevil-like snouts.[22]



Beetle genera were mainly saprophages (detritivores) in the Permian and Triassic. During the Jurassic, herbivorous and then carnivorous genera became more common. In the Cenozoic, genera at all three trophic levels became far more numerous.

In 2009, a fossil beetle was described from the Pennsylvanian of Mazon Creek, Illinois, pushing the origin of the beetles to an earlier date, 318 to 299 mya.[23] Fossils from this time have been found in Asia and Europe, for instance in the red slate fossil beds of Niedermoschel near Mainz, Germany.[24] Further fossils have been found in Obora, Czech Republic and Tshekarda in the Ural mountains, Russia.[25] However, there are only a few fossils from North America before the middle Permian, although both Asia and North America had been united to Euramerica. The first discoveries from North America made in the Wellington formation of Oklahoma were published in 2005 and 2008.[21][26]

As a consequence of the Permian–Triassic extinction event, the fossil record of insects is scant, including beetles from the Lower Triassic.[27] However, there are a few exceptions, such as in Eastern Europe. At the Babiy Kamen site in the Kuznetsk Basin, numerous beetle fossils were discovered, including entire specimens of the infraorders Archostemata (e.g. Ademosynidae, Schizocoleidae), Adephaga (e.g., Triaplidae, Trachypachidae) and Polyphaga (e.g. Hydrophilidae, Byrrhidae, Elateroidea).[28] However, species from the families Cupedidae and Schizophoroidae are not present at this site, whereas they dominate at other fossil sites from the Lower Triassic such as Khey-Yaga, Russia, in the Korotaikha Basin.[21]

Jurassic

During the Jurassic (210 to 145 mya), there was a dramatic increase in the diversity of beetle families,[21] including the development and growth of carnivorous and herbivorous species. The Chrysomeloidea diversified around the same time, feeding on a wide array of plant hosts from cycads and conifers to angiosperms.[29] Close to the Upper Jurassic, the Cupedidae decreased, but the diversity of the early plant-eating species increased. Most recent plant-eating beetles feed on flowering plants or angiosperms, whose success contributed to a doubling of plant-eating species during the Middle Jurassic. However, the increase of the number of beetle families during the Cretaceous does not correlate with the increase of the number of angiosperm species.[30] Around the same time, numerous primitive weevils (e.g. Curculionoidea) and click beetles (e.g. Elateroidea) appeared. The first jewel beetles (e.g. Buprestidae) are present, but they remained rare until the Cretaceous.[31][32][33] The first scarab beetles were not coprophagous but presumably fed on rotting wood with the help of fungus; they are an early example of a mutualistic relationship.

There are more than 150 important fossil sites from the Jurassic, the majority in Eastern Europe and North Asia. Outstanding sites include Solnhofen in Upper Bavaria, Germany,[34] Karatau in South Kazakhstan,[35] the Yixian formation in Liaoning, North China,[36] as well as the Jiulongshan formation and further fossil sites in Mongolia. In North America there are only a few sites with fossil records of insects from the Jurassic, namely the shell limestone deposits in the Hartford basin, the Deerfield basin and the Newark basin.[21][37]

Cretaceous

The Cretaceous saw the fragmenting of the southern landmass, with the opening of the southern Atlantic Ocean and the isolation of New Zealand, while South America, Antarctica, and Australia grew more distant.[29] The diversity of Cupedidae and Archostemata decreased considerably. Predatory ground beetles (Carabidae) and rove beetles (Staphylinidae) began to distribute into different patterns; the Carabidae predominantly occurred in the warm regions, while the Staphylinidae and click beetles (Elateridae) preferred temperate climates. Likewise, predatory species of Cleroidea and Cucujoidea hunted their prey under the bark of trees together with the jewel beetles (Buprestidae). The diversity of jewel beetles increased rapidly, as they were the primary consumers of wood,[38] while longhorn beetles (Cerambycidae) were rather rare: their diversity increased only towards the end of the Upper Cretaceous.[21] The first coprophagous beetles are from the Upper Cretaceous[39] and may have lived on the excrement of herbivorous dinosaurs.[40] The first species where both larvae and adults are adapted to an aquatic lifestyle are found. Whirligig beetles (Gyrinidae) were moderately diverse, although other early beetles (e.g. Dytiscidae) were less, with the most widespread being the species of Coptoclavidae, which preyed on aquatic fly larvae.[21]

Many fossil sites worldwide contain beetles from the Cretaceous. Most are in Europe and Asia and belong to the temperate climate zone during the Cretaceous.[36] Lower Cretaceous sites include the Crato fossil beds in the Araripe basin in the Ceará, North Brazil, as well as overlying Santana formation; the latter was near the equator at that time. In Spain, important sites are near Montsec and Las Hoyas. In Australia, the Koonwarra fossil beds of the Korumburra group, South Gippsland, Victoria, are noteworthy. Major sites from the Upper Cretaceous include Kzyl-Dzhar in South Kazakhstan and Arkagala in Russia.[21]

Cenozoic

Beetle fossils are abundant in the Cenozoic; by the Quaternary (up to 1.6 mya), fossil species are identical to living ones, while from the Late Miocene (5.7 mya) the fossils are still so close to modern forms that they are most likely the ancestors of living species. The large oscillations in climate during the Quaternary caused beetles to change their geographic distributions so much that current location gives little clue to the biogeographical history of a species. It is evident that geographic isolation of populations must often have been broken as insects moved under the influence of changing climate, causing mixing of gene pools, rapid evolution, and extinctions, especially in middle latitudes.[42]

Fossil buprestid beetle from the Eocene (50 mya) Messel pit, which retains its structural color[41]

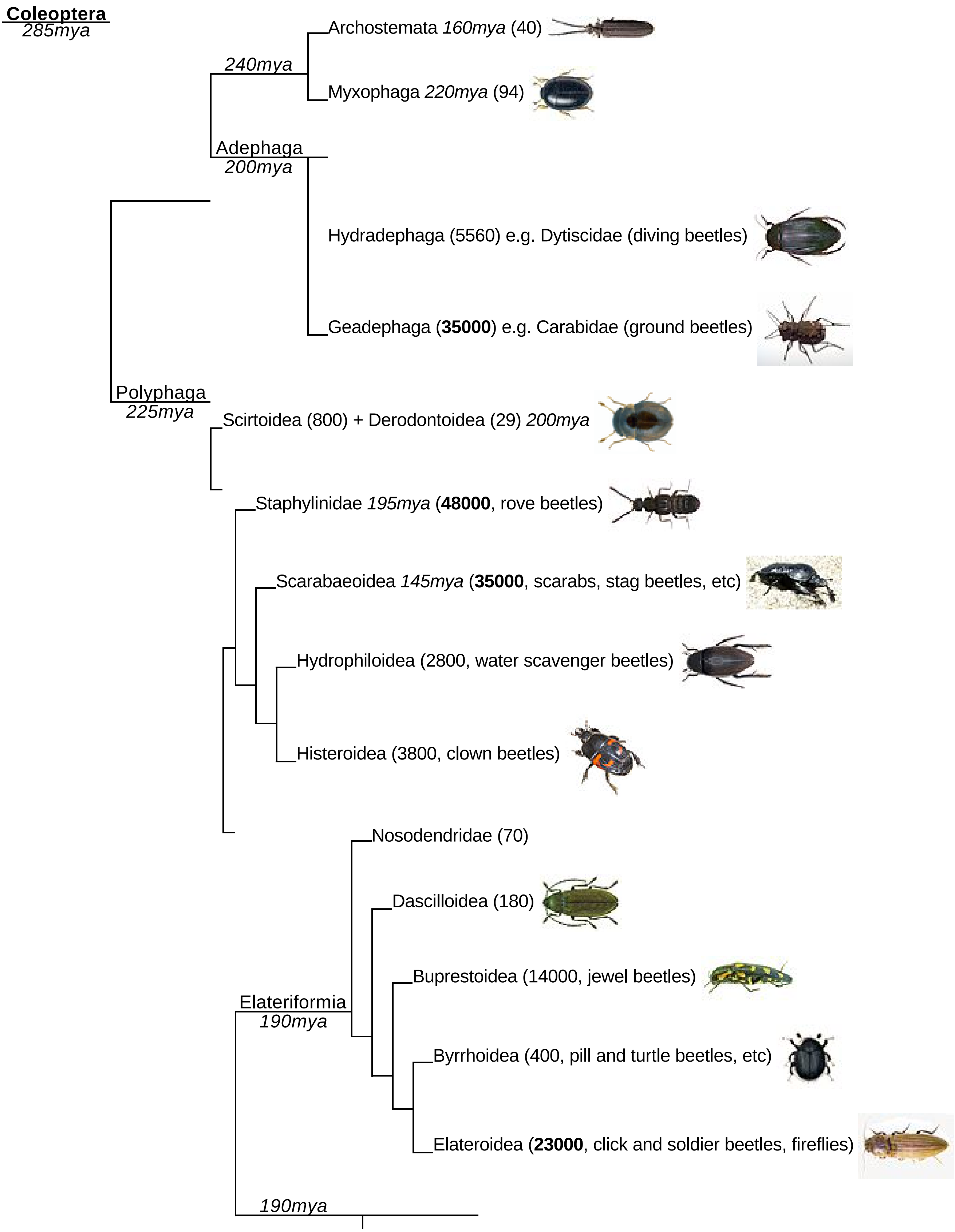
Phylogeny

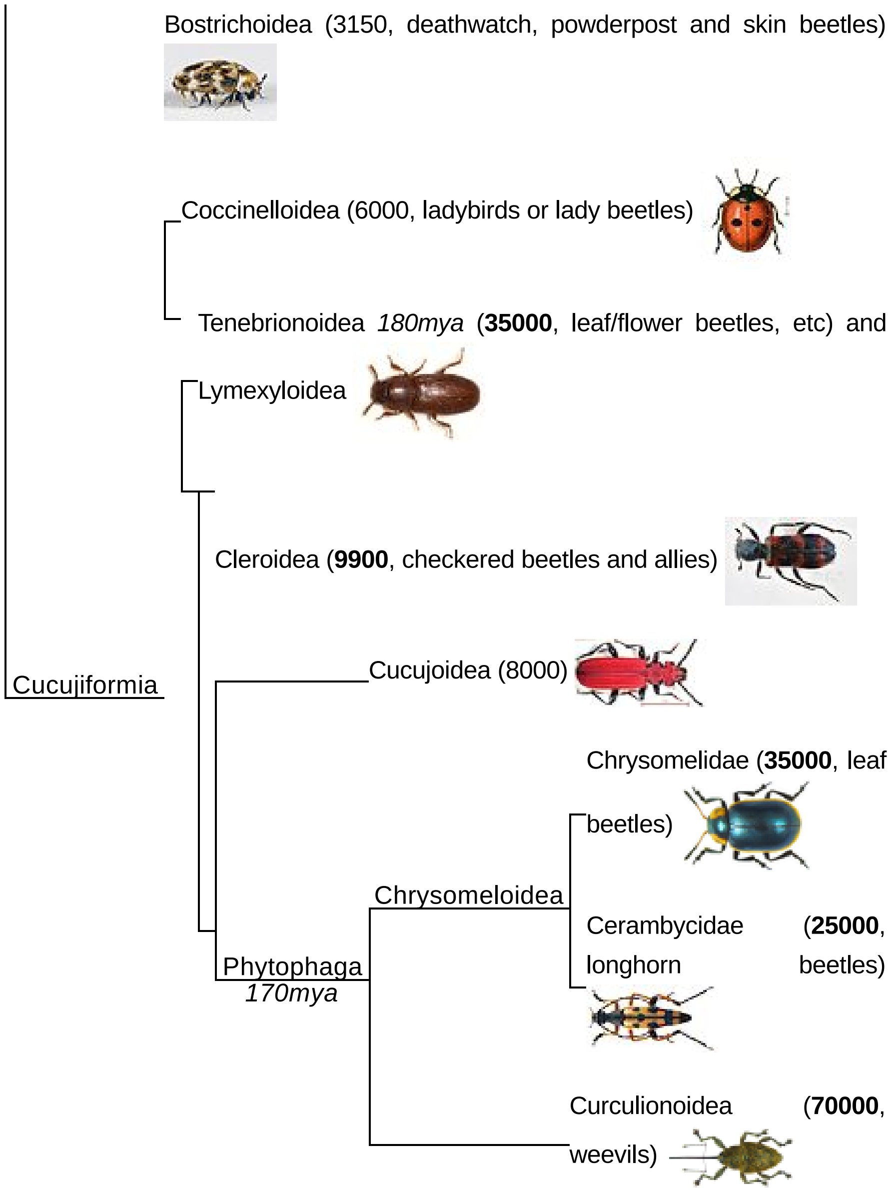
The very large number of beetle species poses special problems for classification. Some families contain tens of thousands of species, and need to be divided into subfamilies and tribes. This immense number led the evolutionary biologist J. B. S. Haldane to quip, when some theologians asked him what could be inferred about the mind of the Creator from the works of His Creation, "An inordinate fondness for beetles".[43] Polyphaga is the largest suborder, containing more than 300,000 described species in more than 170 families, including rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), blister beetles (Meloidae), stag beetles (Lucanidae) and true weevils (Curculionidae).[9][44] These polyphagan beetle groups can be identified by the presence of cervical sclerites (hardened parts of the head used as points of attachment for muscles) absent in the other suborders.[45] Adephaga contains about 10 families of largely predatory beetles, includes ground beetles (Carabidae), water beetles (Dytiscidae) and whirligig beetles (Gyrinidae). In these insects, the testes are tubular and the first abdominal sternum (a plate of the exoskeleton) is divided by the hind coxae (the basal joints of the beetle's legs).[46] Archostemata contains four families of mainly wood-eating beetles, including reticulated beetles (Cupedidae) and the telephone-pole beetle.[47] The Archostemata have an exposed plate called the metatrochantin in front of the basal segment or coxa of the hind leg.[48] Myxophaga contains about 65 described species in four families, mostly very small, including Hydroscaphidae and the genus *Sphaerius*.[49] The myxophagan beetles are small and mostly alga-feeders. Their mouthparts are characteristic in lacking galeae and having a mobile tooth on their left mandible.[50]

The consistency of beetle morphology, in particular their possession of elytra, has long suggested that Coleoptera is monophyletic, though there have been doubts about the arrangement of the suborders, namely the Adephaga, Archostemata, Myxophaga and Polyphaga within that clade.[51][29][52][53][54] The twisted-wing parasites, Strepsiptera, are thought to be a sister group to the beetles, having split from them

in the Early Permian.[53][55][56][57]

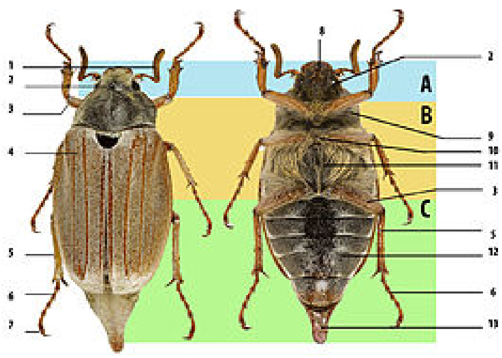
Molecular phylogenetic analysis confirms that the Coleoptera are monophyletic. Duane McKenna et al. (2015) used eight nuclear genes for 367 species from 172 of 183 Coleopteran families. They split the Adephaga into 2 clades, Hydradephaga and Geadephaga, broke up the Cucujoidea into 3 clades, and placed the Lymexyloidea within the Tenebrionoidea. The Polyphaga appear to date from the Triassic. Most extant beetle families appear to have arisen in the Cretaceous.[57] The cladogram is based on McKenna (2015).[57] The number of species in each group (mainly superfamilies) is shown in parentheses, and boldface if over 10,000.[58] English common names are given where possible. Dates of origin of major groups are shown in italics in millions of years ago (mya).[58]





External morphology

Beetles are generally characterized by a particularly hard exoskeleton and hard forewings (elytra) not usable for flying. Almost all beetles have mandibles that move in a horizontal plane. The mouthparts are rarely suctorial, though they are sometimes reduced; the maxillae always bear palps. The antennae usually have 11 or fewer segments, except in some groups like the Cerambycidae (longhorn beetles) and the Rhipiceridae (cicada parasite beetles). The coxae of the legs are usually located recessed within a coxal cavity. The genitalic structures are telescoped into the last abdominal segment in all extant beetles. Beetle larvae can often be confused with those of other endopterygote groups.[48] The beetle's exoskeleton is made up of numerous plates, called sclerites, separated by thin sutures. This design provides armored defenses while maintaining flexibility. The general anatomy of a beetle is quite uniform, although specific organs and appendages vary greatly in appearance and function between the many families in the order. Like all insects, beetles' bodies are divided into three sections: the head, the thorax, and the abdomen.[7] Because there are so many species, identification is quite difficult, and



Beetle body structure, using cockchafer. A: head, B: thorax, C: abdomen. 1: antenna, 2: compound eye, 3: femur, 4: elytron (wing cover), 5: tibia, 6: tarsus, 7: claws, 8: mouthparts, 9: prothorax, 10: mesothorax, 11: metathorax, 12: abdominal sternites, 13: pygidium.

relies on attributes including the shape of the antennae, the tarsal formulae[a] and shapes of these small segments on the legs, the mouthparts, and the ventral plates (sterna, pleura, coxae). In many species accurate identification can only be made by examination of the unique male genitalic structures.[59]

Head

The head, having mouthparts projecting forward or sometimes downturned, is usually heavily sclerotized and is sometimes very large.[6] The eyes are compound and may display remarkable adaptability, as in the case of the aquatic whirligig beetles (Gyrinidae), where they are split to allow a view both above and below the waterline. A few Longhorn beetles (Cerambycidae) and weevils as well as some fireflies (Rhagophthalmidae) [60] have divided eyes, while many have eyes that are notched, and a few have ocelli, small, simple eyes usually farther back on the head (on the vertex); these are more common in larvae than in adults.[61] The anatomical organization of the compound eyes may be modified and depends on whether a species is primarily crepuscular, or diurnally or nocturnally active.[62] Ocelli are found in the adult carpet beetle (Dermestidae), some rove beetles (Omaliinae), and the Derodontidae.[61]

Polyphylla fullo has distinctive fan-like antennae, one of several distinct forms for the appendages among beetles.

Beetle antennae are primarily organs of sensory perception and can detect motion, odour and chemical substances,[63] but may also be used to physically feel a beetle's environment. Beetle families may use antennae in different ways. For example, when moving quickly, tiger beetles may not be able to see very well and instead hold their antennae rigidly in front of them in order to avoid obstacles.[64] Certain Cerambycidae use antennae to balance, and blister beetles may use them for grasping. Some aquatic beetle species may use antennae for gathering air and passing it under the body whilst submerged. Equally, some families use antennae during mating, and a few species use them for defence. In the cerambycid *Onychocerus albitarsis*, the antennae have venom injecting structures used in defence, which is unique among arthropods.[65] Antennae vary greatly in form, sometimes between the sexes, but are often similar within any given family. Antennae may be clubbed, threadlike, angled, shaped like a string of beads, comb-like (either on one side or both, bipectinate), or toothed. The physical variation of antennae is important for the identification of many beetle groups. The Curculionidae have elbowed or geniculate antennae. Feather like flabellate antennae are a restricted form found in the Rhipiceridae and a few other families. The Silphidae have a capitate antennae with a spherical head at the tip. The Scarabaeidae typically have lamellate antennae with the terminal segments extended into long flat structures stacked together. The Carabidae typically have thread-like antennae. The antennae arises between the eye and the mandibles and in the Tenebrionidae, the antennae rise in front of a notch that breaks the usually circular outline of the compound eye. They are segmented and usually consist of 11 parts, the first part is called the scape and the second part is the pedicel. The other segments are jointly called the flagellum.[63][66][67]

Beetles have mouthparts like those of grasshoppers. The mandibles appear as large pincers on the front of some beetles. The mandibles are a pair of hard, often tooth-like structures that move horizontally to grasp, crush, or cut food or enemies (see defence, below). Two pairs of finger-like appendages, the maxillary and labial palpi, are found around the mouth in most beetles, serving to move food into the mouth. In many species, the mandibles are sexually dimorphic, with those of the males enlarged enormously compared with those of females of the same species.[6]

Thorax

The thorax is segmented into the two discernible parts, the pro- and pterothorax. The pterothorax is the fused meso- and metathorax, which are commonly separated in other insect species, although flexibly articulate from the prothorax. When viewed from below, the thorax is that part from which all three pairs of legs and both pairs of wings arise. The abdomen is everything posterior to the thorax.[7] When viewed from above, most beetles appear to have three clear sections, but this is deceptive: on the beetle's upper surface, the middle section is a hard plate called the pronotum, which is only the front part of the thorax; the back part of the thorax is concealed by the beetle's wings. This further segmentation is usually best seen on the abdomen.[68]

Legs

The multisegmented legs end in two to five small segments called tarsi. Like many other insect orders, beetles have claws, usually one pair, on the end of the last tarsal segment of each leg. While most beetles use their legs for walking, legs have been variously adapted for other uses. Aquatic beetles including the Dytiscidae (diving beetles), Haliplidae, and many species of Hydrophilidae, the legs, often the last pair, are modified for swimming, typically with rows of long hairs. Male diving beetles have suctorial cups on their forelegs that they use to grasp females.[69] Other beetles have fossorial legs widened and often spined for digging. Species with such adaptations are found among the scarabs, ground beetles, and clown beetles (Histeridae). The hind legs of some beetles, such as flea beetles (within Chrysomelidae) and flea weevils (within Curculionidae), have enlarged femurs that help them leap.[70]

Acilius sulcatus, a diving beetle with hind legs adapted as swimming limbs

Wings

Checkered beetle *Trichodes alvearius* taking off, showing the hard elytra (forewings adapted as wing-cases) held stiffly away from the flight wings

The forewings of beetles are not used for flight, but form elytra which cover the hind part of the body and protect the hindwings. The elytra are usually hard shell-like structures which must be raised to allow the hind wings to move for flight.[71] However, in the soldier beetles (Cantharidae), the elytra are soft, earning this family the name of leatherwings.[72] Other soft wing beetles include the net-winged beetle *Calopteron discrepans*, which has brittle wings that rupture easily in order to release chemicals for defence.[73]

Beetles' flight wings are crossed with veins and are folded after landing, often along these veins, and stored below the elytra. A fold (*jugum*) of the membrane at the base of each wing is characteristic.[71] Some beetles have lost the ability to fly. These include some ground beetles (Carabidae) and some true weevils (Curculionidae), as well as desert- and cave-dwelling species of other families. Many have the two elytra fused together, forming a solid shield over the abdomen. In a few families, both the ability to fly and the elytra have been lost, as in the glow-worms (Phengodidae), where the females resemble larvae throughout their lives.[74] The presence of elytra and wings does not always indicate that the beetle will fly. For example, the tansy beetle walks between habitats despite being physically capable of flight.[75]

Abdomen

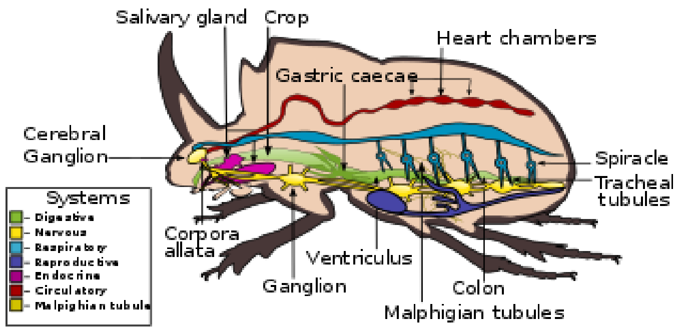
The abdomen is the section behind the metathorax, made up of a series of rings, each with a hole for breathing and respiration, called a spiracle, composing three different segmented sclerites: the tergum, pleura, and the sternum. The tergum in almost all species is membranous, or usually soft and concealed by the wings and elytra when not in flight. The pleura are usually small or hidden in some species, with each pleuron having a single spiracle. The sternum is the most widely visible part of the abdomen, being a more or less sclerotized segment. The abdomen itself does not have any appendages, but some (for example, Mordellidae) have articulating sternal lobes.[76]

Anatomy and physiology

Digestive system

The digestive system of beetles is primarily adapted for a herbivorous diet. Digestion takes place mostly in the anterior midgut, although in predatory groups like the Carabidae, most digestion occurs in the crop by means of midgut enzymes. In the Elateridae, the larvae are liquid feeders that extraorally digest their food by secreting enzymes.[7] The alimentary canal basically consists of a short, narrow pharynx, a widened expansion, the crop, and a poorly developed gizzard. This is followed by the midgut, that varies in dimensions

between species, with a large amount of cecum, and the hindgut, with varying lengths. There are typically four to six Malpighian tubules.[6]



A beetle's body systems

Nervous system

The nervous system in beetles contains all the types found in insects, varying between different species, from three thoracic and seven or eight abdominal ganglia which can be distinguished to that in which all the thoracic and abdominal ganglia are fused to form a composite structure.[7]

Respiratory system

Dytiscus spiracles (right) on upper side of abdomen, normally covered by the elytra, are in contact with an air bubble when the beetle dives.

Like most insects, beetles inhale air, for the oxygen it contains, and exhale carbon dioxide, via a tracheal system. Air enters the body through spiracles, and circulates within the haemocoel in a system of tracheae and tracheoles, through whose walls the gases can diffuse.[7]

Diving beetles, such as the Dytiscidae, carry a bubble of air with them when they dive. Such a bubble may be contained under the elytra or against the body by specialized hydrophobic hairs. The bubble covers at least some of the spiracles, permitting air to enter the tracheae.[7] The function of the bubble is not only to contain a store of air but to act as a physical gill. The air that it traps is in contact with oxygenated water, so as the animal's consumption depletes the oxygen in the bubble, more oxygen can diffuse in to replenish it.[77] Carbon dioxide is more soluble in water than either oxygen or nitrogen, so it readily diffuses out faster than in. Nitrogen is the most plentiful gas in the bubble, and the least soluble, so it constitutes a relatively static component of the bubble and acts as a stable medium for respiratory gases to accumulate in and pass through. Occasional visits to the surface are sufficient for the beetle to re-establish the constitution of the bubble.[78]

Circulatory system

Like other insects, beetles have open circulatory systems, based on hemolymph rather than blood. As in other insects, a segmented tube-like heart is attached to the dorsal wall of the hemocoel. It has paired inlets or *ostia* at intervals down its length, and circulates the hemolymph from the main cavity of the haemocoel and out through the anterior cavity in the head.[79]

Specialized organs

Different glands are specialized for different pheromones to attract mates. Pheromones from species of Rutelinae are produced from epithelial cells lining the inner surface of the apical abdominal segments; amino acid-based pheromones of Melolonthinae are produced from eversible glands on the abdominal apex. Other species produce different types of pheromones. Dermestids produce esters, and species of Elateridae produce fatty acid-derived aldehydes and acetates.[7] To attract a mate, fireflies (Lampyridae) use modified fat body cells with transparent surfaces backed with reflective uric acid crystals to produce light by bioluminescence. Light production is highly efficient, by oxidation of luciferin catalyzed by enzymes (luciferases) in the presence of adenosine triphosphate (ATP) and oxygen, producing oxyluciferin, carbon dioxide, and light.[7]

Tympanal organs or hearing organs consist of a membrane (tympanum) stretched across a frame backed by an air sac and associated sensory neurons, are found in two families.[80] Several species of the genus *Cicindela* (Carabidae) have hearing organs on the dorsal surfaces of their first abdominal segments beneath the wings; two tribes in the Dynastinae (within the Scarabaeidae) have hearing organs just beneath their pronotal shields or neck membranes. Both families are sensitive to ultrasonic frequencies, with strong evidence indicating they function to detect the presence of bats by their ultrasonic echolocation.[7]

Reproduction and development

Beetles are members of the superorder Endopterygota, and accordingly most of them undergo complete metamorphosis. The typical form of metamorphosis in beetles passes through four main stages: the egg, the larva, the pupa, and the imago or adult. The larvae are commonly called grubs and the pupa sometimes is called the chrysalis. In some species, the pupa may be enclosed in a cocoon constructed by the larva towards the end of its final instar. Some beetles, such as typical members of the families Meloidae and Rhipiphoridae, go further, undergoing hypermetamorphosis in which the first instar takes the form of a triungulin.[81]

Mating

Punctate flower chafers (*Neorrhina punctata*, Scarabaeidae) mating

Some beetles have intricate mating behaviour. Pheromone communication is often important in locating a mate. Different species use different pheromones. Scarab beetles such as the Rutelinae use pheromones derived from fatty acid synthesis, while other scarabs such as the Melolonthinae use amino acids and terpenoids. Another way beetles find mates is seen in the fireflies (Lampyridae) which are bioluminescent, with abdominal light-producing organs. The males and females engage in a complex dialogue before mating; each species has a unique combination of flight patterns, duration, composition, and intensity of the light produced.[7]

Before mating, males and females may stridulate, or vibrate the objects they are on. In the Meloidae, the male climbs onto the dorsum of the female and strokes his antennae on her head, palps, and antennae. In *Eupompha*, the male draws his antennae along his longitudinal vertex. They may not mate at all if they do not perform the precopulatory ritual.[7] This mating behaviour may be different amongst dispersed populations of the same species. For example, the mating of a Russian population of tansy beetle (*Chysolina graminis*) is preceded by an elaborate ritual involving the male tapping the female's eyes, pronotum and antennae with its antennae, which is not evident in the population of this species in the United Kingdom.[82]

Competition can play a part in the mating rituals of species such as burying beetles (*Nicrophorus*), the insects fighting to determine which can mate. Many male beetles are territorial and fiercely defend their territories from intruding males. In such species, the male often has horns on the head or thorax, making its body length greater than that of a female. Copulation is generally quick, but in some cases lasts for several hours. During copulation, sperm cells are transferred to the female to fertilize the egg.[6]

Life cycle

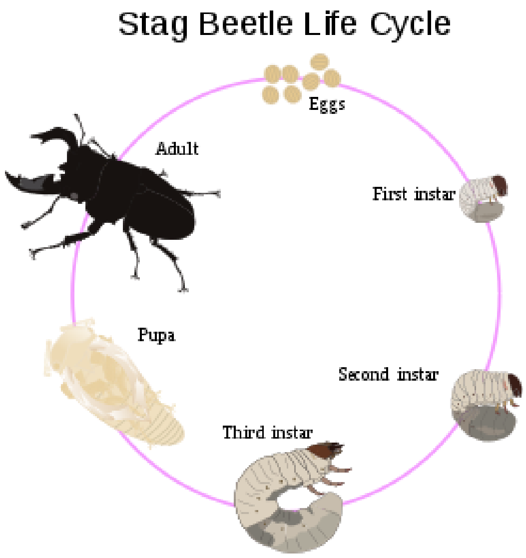
Egg

Essentially all beetles lay eggs, though some myrmecophilous Aleocharinae and some Chrysomelinae which live in mountains or the subarctic are ovoviviparous, laying eggs which hatch almost immediately. Beetle eggs generally have smooth surfaces and are soft, though the Cupedidae have hard eggs. Eggs vary widely between species: the eggs tend to be small in species with many instars (larval stages), and in those that lay large numbers of eggs. A female may lay from several dozen to several thousand eggs during her lifetime, depending on the extent of parental care. This ranges from the simple laying of eggs under a leaf, to the parental care provided by scarab beetles, which house, feed and protect their young. The Attelabidae roll leaves and lay their eggs inside the roll for protection.[7][83]

Larva

The larva is usually the principal feeding stage of the beetle life cycle. Larvae tend to feed voraciously once they emerge from their eggs. Some feed externally on plants, such as those of certain leaf beetles, while others feed within their food sources. Examples of internal feeders are most Buprestidae and longhorn beetles. The larvae of many beetle families are predatory like the adults (ground beetles, ladybirds, rove beetles). The larval period varies between species, but can be as long as several years. The larvae of skin beetles undergo a degree of reversed development when starved, and later grow back to the previously attained level of maturity. The cycle can be repeated

many times (see Biological immortality).[84] Larval morphology is highly varied amongst species, with well-developed and sclerotized heads, distinguishable thoracic and abdominal segments (usually the tenth, though sometimes the eighth or ninth).[6]



The life cycle of the stag beetle includes three instars.


Scarabaeiform larva of Hercules beetle

Beetle larvae can be differentiated from other insect larvae by their hardened, often darkened heads, the presence of chewing mouthparts, and spiracles along the sides of their bodies. Like adult beetles, the larvae are varied in appearance, particularly between beetle families. Beetles with somewhat flattened, highly mobile larvae include the ground beetles and rove beetles; their larvae are described as campodeiform. Some beetle larvae resemble hardened worms with dark head capsules and minute legs. These are elateriform larvae, and are found in the click beetle (Elateridae) and darkling beetle (Tenebrionidae) families. Some elateriform larvae of click beetles are known as wireworms. Beetles in the Scarabaeoidea have short, thick larvae described as scarabaeiform, more commonly known as grubs.[85]

All beetle larvae go through several instars, which are the developmental stages between each moult. In many species, the larvae simply increase in size with each successive instar as more food is consumed. In some cases, however, more dramatic changes occur. Among certain beetle families or genera, particularly those that exhibit parasitic lifestyles, the first instar (the planidium) is highly mobile to search out a host, while the following instars are more sedentary and remain on or within their host. This is known as hypermetamorphosis; it occurs in the Meloidae, Micromalthidae, and Ripiphoridae.[86] The blister beetle *Epicauta vittata* (Meloidae), for example, has three distinct larval stages. Its first stage, the triungulin, has longer legs to go in search of the eggs of grasshoppers. After feeding for a week it moults to the second stage, called the caraboid stage, which resembles the larva of a carabid beetle. In another week it moults and assumes the appearance of a scarabaeid larva – the scarabaeidoid stage. Its penultimate larval stage is the pseudo-pupa or the coarcate larva, which will overwinter and pupate until the next spring.[87]

The larval period can vary widely. A fungus feeding staphylinid *Phanerota fasciata* undergoes three moults in 3.2 days at room temperature while *Anisotoma* sp. (Leiodidae) completes its larval stage in the fruiting body of slime mold in 2 days and possibly represents the fastest growing beetles. Dermestid beetles, *Trogoderma inclusum* can remain in an extended larval state under unfavourable conditions, even reducing their size between moults. A larva is reported to have survived for 3.5 years in an enclosed container.[7]

Pupa and adult

As with all endopterygotes, beetle larvae pupate, and from these pupae emerge fully formed, sexually mature adult beetles, or imagos. Pupae never have mandibles (they are adecticous). In most pupae, the appendages are not attached to the body and are said to be exarate; in a few beetles (Staphylinidae, Ptiliidae etc.) the appendages are fused with the body (termed as obtect pupae).[6]

Adults have extremely variable lifespans, from weeks to years, depending on the species.[6][48] Some wood-boring beetles can have extremely long life-cycles. It is believed that when furniture or house timbers are infested by beetle larvae, the timber already contained the larvae when it was first sawn up. A birch bookcase 40 years old released adult *Eburia quadrigeminata* (Cerambycidae), while *Buprestis aurulenta* and other Buprestidae have been documented as emerging as much as 51 years after manufacture of wooden items.[88]

Behaviour

Locomotion

Photinus pyralis, firefly, in flight

The ivory-marked beetle, *Eburia quadrigeminata*, may live up to 40 years inside the hardwoods on which the larva feeds.

The elytra allow beetles to both fly and move through confined spaces, doing so by folding the delicate wings under the elytra while not flying, and folding their wings out just before takeoff. The unfolding and folding of the wings is operated by muscles attached to the wing base; as long as the tension on the radial and cubital veins remains, the wings remain straight. In some day-flying species (for example, Buprestidae, Scarabaeidae), flight does not include large amounts of lifting of the elytra, having the metathorac wings extended under the lateral elytra margins.[7] The altitude reached by beetles in flight varies. One study investigating the flight altitude of the ladybird species *Coccinella septempunctata* and *Harmonia axyridis* using radar showed that, whilst the majority in flight over a single location were at 150–195 m above ground level, some reached altitudes of over 1100 m.[89]

Many rove beetles have greatly reduced elytra, and while they are capable of flight, they most often move on the ground: their soft bodies and strong abdominal muscles make them flexible, easily able to wriggle into small cracks.[90]

Aquatic beetles use several techniques for retaining air beneath the water's surface. Diving beetles (Dytiscidae) hold air between the abdomen and the elytra when diving. Hydrophilidae have hairs on their under surface that retain a layer of air against their bodies. Adult crawling water beetles use both their elytra and their hind coxae (the basal segment of the back legs) in air retention, while whirligig beetles simply carry an air bubble down with them whenever they dive.[91]

Communication

Beetles have a variety of ways to communicate, including the use of pheromones. The mountain pine beetle emits a pheromone to attract other beetles to a tree. The mass of beetles are able to overcome the chemical defenses of the tree. After the tree's defenses have been exhausted, the beetles emit an anti-aggregation pheromone. This species can stridulate to communicate,[92] but others may use sound to defend themselves when attacked.[93]

Parental care

A dung beetle rolling dung

Parental care is found in a few families[94] of beetle, perhaps for protection against adverse conditions and predators.[7] The rove beetle *Bledius spectabilis* lives in salt marshes, so the eggs and larvae are endangered by the rising tide. The maternal beetle patrols the eggs and larvae, burrowing to keep them from flooding and asphyxiating, and protects them from the predatory carabid beetle *Dicheirotrichus gustavi* and from the parasitoidal wasp *Barycnemis blediator*, which kills some 15% of the larvae.[95]

Burying beetles are attentive parents, and participate in cooperative care and feeding of their offspring. Both parents work to bury small animal carcass to serve as a food resource for their young and build a brood chamber around it. The parents prepare the carcass and protect it from competitors and from early decomposition. After their eggs hatch, the parents keep the larvae clean of fungus and bacteria and help the larvae feed by regurgitating food for them.[96]

Some dung beetles provide parental care, collecting herbivore dung and laying eggs within that food supply, an instance of mass provisioning. Some species do not leave after this stage, but remain to safeguard their offspring.[97]

Most species of beetles do not display parental care behaviors after the eggs have been laid.[98]

Subsociality, where females guard their offspring, is well-documented in two families of Chrysomelidae, Cassidinae and Chrysomelinae.[99][100][101][102][103]

Eusociality

Eusociality involves cooperative brood care (including brood care of offspring from other individuals), overlapping generations within a colony of adults, and a division of labour into reproductive and non-reproductive groups.[104] Few organisms outside Hymenoptera exhibit this behavior; the only beetle to do so is the weevil *Austroplatypus incompertus*.[105] This Australian species lives in horizontal networks of tunnels, in the heartwood of *Eucalyptus* trees. It is one of more than 300 species of wood-boring Ambrosia beetles which distribute the spores of ambrosia fungi.[106] The fungi grow in the beetles' tunnels, providing food for the beetles and their larvae; female offspring remain in the tunnels and maintain the fungal growth, probably never reproducing.[106][105] Cooperative brood care is also found in the bess beetles (Passalidae) where the larvae feed on the semi-digested faeces of the adults.[107]

Feeding

Hycleus sp. (Meloidae) feeding on the petals of *Ipomoea carnea*

Beetles are able to exploit a wide diversity of food sources available in their many habitats. Some are omnivores, eating both plants and animals. Other beetles are highly specialized in their diet. Many species of leaf beetles, longhorn beetles, and weevils are very host-specific, feeding on only a single species of plant. Ground beetles and rove beetles (Staphylinidae), among others, are primarily carnivorous and catch and consume many other arthropods and small prey, such as earthworms and snails. While most predatory beetles are generalists, a few species have more specific prey requirements or preferences.[108]

Decaying organic matter is a primary diet for many species. This can range from dung, which is consumed by coprophagous species (such as certain scarab beetles in the Scarabaeidae), to dead animals, which are eaten by necrophagous species (such as the carrion beetles, Silphidae). Some beetles found in dung and carrion are in fact predatory. These include members of the Histeridae and Silphidae, preying on the larvae of coprophagous and necrophagous insects.[109] Many beetles feed under bark, some feed on wood while others feed on fungi growing on wood or leaf-litter. Some beetles have special mycangia, structures for the transport of fungal spores.[110]

Ecology

Anti-predator adaptations

A camouflaged longhorn beetle, *Ecyrus dasycerus*

Beetles, both adults and larvae, are the prey of many animal predators including mammals from bats to rodents, birds, lizards, amphibians, fishes, dragonflies, robberflies, reduviid bugs, ants, other beetles, and spiders.[111][112] Beetles use a variety of anti-predator adaptations to defend themselves. These include camouflage and mimicry against predators that hunt by sight, toxicity, and defensive behaviour.

Camouflage

Camouflage is common and widespread among beetle families, especially those that feed on wood or vegetation, such as leaf beetles (Chrysomelidae, which are often green) and weevils. In some species, sculpturing or various coloured scales or hairs cause beetles such as the avocado weevil *Heilipus apiatus* to resemble bird dung or other inedible objects.[111] Many beetles that live in sandy environments blend in with the coloration of that substrate.[113]

Mimicry and aposematism

Clytus arietis (Cerambycidae), a Batesian mimic of wasps

Some longhorn beetles (Cerambycidae) are effective Batesian mimics of wasps. Beetles may combine coloration with behavioural mimicry, acting like the wasps they already closely resemble. Many other beetles, including ladybirds, blister beetles, and lycid beetles secrete distasteful or toxic substances to make them unpalatable or poisonous, and are often aposematic, where bright or contrasting coloration warn off predators; many beetles and other insects mimic these chemically protected species.[114]

Blister beetles such as *Hycleus* have brilliant aposematic coloration, warning of their toxicity.

The bloody-nosed beetle, *Timarcha tenebricosa*, defending itself by releasing a droplet of noxious red liquid (base of leg, on right)

Chemical defense is important in some species, usually being advertised by bright aposematic colours. Some Tenebrionidae use their posture for releasing noxious chemicals to warn off predators. Chemical defences may serve purposes other than just protection from vertebrates, such as protection from a wide range of microbes. Some species sequester chemicals from the plants they feed on, incorporating them into their own defenses.[113]

Other species have special glands to produce deterrent chemicals. The defensive glands of carabid ground beetles produce a variety of hydrocarbons, aldehydes, phenols, quinones, esters, and acids released from an opening at the end of the abdomen. African carabid beetles (for example, *Anthia* and *Thermophilum* – *Thermophilum* is sometimes included within *Anthia*) employ the same chemicals as ants: formic acid.[114] Bombardier beetles have well-developed pygidial glands that empty from the sides of the intersegment membranes between the seventh and eighth abdominal segments. The gland is made of two containing chambers, one for hydroquinones and hydrogen peroxide, the other holding hydrogen peroxide and catalase enzymes. These chemicals mix and result in an explosive ejection, reaching a temperature of around 100 °C (212 °F), with the breakdown of hydroquinone to hydrogen, oxygen, and quinone. The oxygen propels the noxious chemical spray as a jet that can be aimed accurately at predators.[7]

Other defences

Large ground-dwelling beetles such as Carabidae, the rhinoceros beetle and the longhorn beetles defend themselves using strong mandibles, or heavily sclerotised (armored) spines or horns to deter or fight off predators.[113] Many species of weevil that feed out in the open on leaves of plants react to attack by employing a drop-off reflex. Some combine it with thanatosis, in which they close up their appendages and "play dead".[115] The click beetles (Elateridae) can suddenly catapult themselves out of danger by releasing the energy stored by a click mechanism, which consists of a stout spine on the prosternum and a matching groove in the mesosternum.[111] Some species startle an attacker by producing sounds through a process known as stridulation.[93]

Parasitism

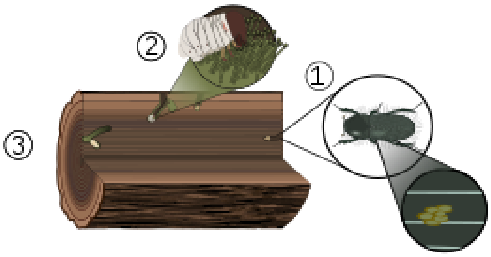
A few species of beetles are ectoparasitic on mammals. One such species, *Platypsyllus castoris*, parasitises beavers (*Castor* spp.). This beetle lives as a parasite both as a larva and as an adult, feeding on epidermal tissue and possibly on skin secretions and wound exudates. They are strikingly flattened dorsoventrally, no doubt as an adaptation for slipping between the beavers' hairs. They are wingless and eyeless, as are many other ectoparasites.[116] Others are kleptoparasites of other invertebrates, such as the small hive beetle (*Aethina tumida*) that infests honey bee nests,[117] while many species are parasitic inquilines or commensal in the nests of ants.[118] A few groups of beetles are primary parasitoids of other insects, feeding off of, and eventually killing their hosts.[119]

Pollination

Beetle-pollinated flowers are usually large, greenish or off-white in color, and heavily scented. Scents may be spicy, fruity, or similar to decaying organic material. Beetles were most likely the first insects to pollinate flowers. Most beetle-pollinated flowers are flattened or dish-shaped, with pollen easily accessible, although they may include traps to keep the beetle longer. The plants' ovaries are usually well protected from the biting mouthparts of their pollinators. The beetle families that habitually pollinate flowers are the Buprestidae, Cantharidae, Cerambycidae, Cleridae, Dermestidae, Lycidae, Melyridae, Mordellidae, Nitidulidae and Scarabaeidae.[120] Beetles may be particularly important in some parts of the world such as semiarid areas of southern Africa and southern California[121] and the montane grasslands of KwaZulu-Natal in South Africa.[122]


An Israeli Copper Flower-Chafer (*Protaetia cuprea ignicollis*) pollinating a crown daisy (*Glebionis coronaria*)

Mutualism


1: Adult ambrosia beetle burrows into wood and lays eggs, carrying fungal spores in its mycangia.
2: Larva feeds on fungus, which digests wood, removing toxins, to mutual benefit.
3: Larva pupates.

Mutualism is well known in a few beetles, such as the ambrosia beetle, which partners with fungi to digest the wood of dead trees. The beetles excavate tunnels in dead trees in which they cultivate fungal gardens, their sole source of nutrition. After landing on a suitable tree, an ambrosia beetle excavates a tunnel in which it releases spores of its fungal symbiont. The fungus penetrates the plant's xylem tissue, digests it, and concentrates the nutrients on and near the surface of the beetle gallery, so the weevils and the fungus both benefit. The beetles cannot eat the wood due to toxins, and uses its relationship with fungi to help overcome the defenses of its host tree in order to provide nutrition for their larvae.[123] Chemically mediated by a bacterially produced polyunsaturated peroxide,[124] this mutualistic relationship between the beetle and the fungus is coevolved.[123][125]

Tolerance of extreme environments


Beetle found in Thar Desert

About 90% of beetle species enter a period of adult diapause, a quiet phase with reduced metabolism to tide unfavourable environmental conditions. Adult diapause is the most common form of diapause in Coleoptera. To endure the period without food (often lasting many months) adults prepare by accumulating reserves of lipids, glycogen, proteins and other substances needed for resistance to future hazardous changes of environmental conditions. This diapause is induced by signals heralding the arrival of the unfavourable season; usually the cue is photoperiodic. Short (decreasing) day length serves as a signal of approaching winter and induces winter diapause (hibernation).[126] A study of hibernation in the Arctic beetle *Pterostichus brevicorni* showed that the body fat levels of adults were highest in autumn with the alimentary canal filled with food, but empty by the end of January. This loss of body fat was a gradual process, occurring in combination with dehydration.[127]

All insects are poikilothermic,[128] so the ability of a few beetles to live in extreme environments depends on their resilience to unusually high or low temperatures. The bark beetle *Pityogenes chalcographus* can survive −39 °C whilst overwintering beneath tree bark;[129] the Alaskan beetle *Cucujus clavipes puniceus* is able to withstand −58 °C; its larvae may survive −100 °C.[130] At these low temperatures, the formation of ice crystals in internal fluids is the biggest threat to survival to beetles, but this is prevented through the production of antifreeze proteins that stop water molecules from grouping together. The low temperatures experienced by *Cucujus clavipes* can be survived through their deliberate dehydration in conjunction with the antifreeze proteins. This concentrates the antifreezes several fold.[131] The hemolymph of the mealworm beetle *Tenebrio molitor* contains several antifreeze proteins.[132] The Alaskan beetle *Upis ceramboides* can survive −60 °C: its cryoprotectants are xylomannan, a molecule consisting of a sugar bound to a fatty acid,[133] and the sugar-alcohol, threitol.[134]

Conversely, desert dwelling beetles are adapted to tolerate high temperatures. For example, the Tenebrionid beetle *Onymacris rugatipennis* can withstand 50 °C.[135] Tiger beetles in hot, sandy areas are often whitish (for example, *Habroscelimorpha dorsalis*), to reflect more heat than a darker colour would. These beetles also exhibits behavioural adaptions to tolerate the heat: they are able to stand erect on their tarsi to hold their bodies away from the hot ground, seek shade, and turn to face the sun so that only the front parts of their heads are directly exposed.[136]

The fogstand beetle of the Namib Desert, *Stenocara gracilipes* is able to survive by collecting water from fog on its back.

The fogstand beetle of the Namib Desert, *Stenocara gracilipes*, is able to collect water from fog, as its elytra have a textured surface combining hydrophilic (water-loving) bumps and waxy, hydrophobic troughs. The beetle faces the early morning breeze, holding up its abdomen; droplets condense on the elytra and run along ridges towards their mouthparts. Similar adaptations are found in several other Namib desert beetles such as *Onymacris unguicularis*.[137]

Some terrestrial beetles that exploit shoreline and floodplain habitats have physiological adaptations for surviving floods. In the event of flooding, adult beetles may be mobile enough to move away from flooding, but larvae and pupa often cannot. Adults of *Cicindela togata* are unable to survive immersion in water, but larvae are able to survive a prolonged period, up to 6 days, of anoxia during floods. Anoxia tolerance in the larvae may have been sustained by switching to anaerobic metabolic pathways or by reducing metabolic rate.[138] Anoxia tolerance in the adult Carabid beetle *Pelophilia borealis* was tested in laboratory conditions and it was found that they could survive a continuous period of up to 127 days in an atmosphere of 99.9% nitrogen at 0 °C.[139]

Migration

Many beetle species undertake annual mass movements which are termed as migrations. These include the pollen beetle *Meligethes aeneus*[140] and many species of coccinellids.[141] These mass movements may also be opportunistic, in search of food, rather than seasonal. A 2008 study of an unusually large outbreak of Mountain Pine Beetle (*Dendroctonus ponderosae*) in British Columbia found that beetles were capable of flying 30–110 km per day in densities of up to 18, 600 beetles per hectare.[142]

Relationship to humans

In ancient cultures

ḫpr
in hieroglyphs

Several species of dung beetle, especially the sacred scarab, *Scarabaeus sacer*, were revered in Ancient Egypt.[143][144] The hieroglyphic image of the beetle may have had existential, fictional, or ontologic significance.[145] Images of the scarab in bone, ivory, stone, Egyptian faience, and precious metals are known from the Sixth Dynasty and up to the period of Roman rule. The scarab was of prime significance in the funerary cult of ancient Egypt.[146] The scarab was linked to Khepri, the god of the rising sun, from the supposed resemblance of the rolling of the dung ball by the beetle to the rolling of the sun by the god.[143] Some of ancient Egypt's neighbors adopted the scarab motif for seals of varying types. The best-known of these are the Judean LMLK seals, where eight of 21 designs contained scarab beetles, which were used exclusively to stamp impressions on storage jars during the reign of Hezekiah.[147] Beetles are mentioned as a symbol of the sun, as in ancient Egypt, in Plutarch's 1st century *Moralia*.[148] The Greek Magical Papyri of the 2nd century BC to the 5th century AD describe scarabs as an ingredient in a spell.[149]

A scarab in the Valley of the Kings

Pliny the Elder discusses beetles in his *Natural History*,[150] describing the stag beetle: "Some insects, for the preservation of their wings, are covered with a erust (elytra) – the beetle, for instance, the wing of which is peculiarly fine and frail. To these insects a sting has been denied by Nature; but in one large kind we find horns of a remarkable length, two-pronged at the extremities, and forming pincers, which the animal closes when it is its intention to bite."[151][152] The stag beetle is recorded in a Greek myth by Nicander and recalled by Antoninus Liberalis in which Cerambus[b] is turned into a beetle: "He can be seen on trunks and has hook-teeth, ever moving his jaws together. He is black, long and has hard wings like a great dung beetle".[153] The story concludes with the comment that the beetles were used as toys by young boys, and that the head was removed and worn as a pendant.[152][154]

As pests

Cotton boll weevil

About 75% of beetle species are phytophagous in both the larval and adult stages. Many feed on economically important plants and stored plant products, including trees, cereals, tobacco, and dried fruits.[6] Some, such as the boll weevil, which feeds on cotton buds and flowers, can cause extremely serious damage to agriculture. The boll weevil crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico around 1892,[155] and had reached southeastern Alabama by 1915. By the mid-1920s, it had entered all cotton-growing regions in the US, traveling 40 to 160 miles (60–260 km) per year. It remains the most destructive cotton pest in North America. Mississippi State University has estimated, since the boll weevil entered the United States, it has cost cotton producers about $13 billion, and in recent times about $300 million per year.[155]

The bark beetle, elm leaf beetle and the Asian longhorned beetle (*Anoplophora glabripennis*)[156] are among the species that attack elm trees. Bark beetles (Scolytidae) carry Dutch elm disease as they move from infected breeding sites to healthy trees. The disease has devastated elm trees across Europe and North America.[157]

Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata*, a serious crop pest

Some species of beetle have evolved immunity to insecticides. For example, the Colorado potato beetle, *Leptinotarsa decemlineata*, is a destructive pest of potato plants. Its hosts include other members of the Solanaceae, such as nightshade, tomato, eggplant and capsicum, as well as the potato. Different populations have between them developed resistance to all major classes of insecticide.[158] The Colorado potato beetle was evaluated as a tool of entomological warfare during World War II, the idea being to use the beetle and its larvae to damage the crops of enemy nations.[159] Germany tested its Colorado potato beetle weaponisation program south of Frankfurt, releasing 54,000 beetles.[160]

The death watch beetle, *Xestobium rufovillosum* (Ptinidae), is a serious pest of older wooden buildings in Europe. It attacks hardwoods such as oak and chestnut, always where some fungal decay has taken or is taking place. The actual introduction of the pest into buildings is thought to take place at the time of construction.[161]

Other pests include the coconut hispine beetle, *Brontispa longissima*, which feeds on young leaves, seedlings and mature coconut trees, causing serious economic damage in the Philippines.[162] The mountain pine beetle is a destructive pest of mature or weakened lodgepole pine, sometimes affecting large areas of Canada.[163]

As beneficial resources

Beetles can be beneficial to human economics by controlling the populations of pests. The larvae and adults of some species of lady beetles (Coccinellidae) feed on aphids that are pests. Other lady beetles feed on scale insects, whitefly and mealybugs.[164] If normal food sources are scarce, they may feed on small caterpillars, young plant bugs, or honeydew and nectar.[165] Ground beetles (Carabidae) are common predators of many insect pests, including fly eggs, caterpillars, and wireworms.[166] Ground beetles can help to control weeds by eating their seeds in the soil, reducing the need for herbicides to protect crops.[167] The effectiveness of some species in reducing certain

Coccinella septempunctata, a predatory beetle beneficial to agriculture

plant populations has resulted in the deliberate introduction of beetles in order to control weeds. For example, the genus *Zygogramma* is native to North America but has been used to control *Parthenium hysterophorus* in India and *Ambrosia artemisiifolia* in Russia.[168][169]

Dung beetles (Scarabidae) have been successfully used to reduce the populations of pestilent flies, such as *Musca vetustissima* and *Haematobia exigua* which are serious pests of cattle in Australia.[170] The beetles make the dung unavailable to breeding pests by quickly rolling and burying it in the soil, with the added effect of improving soil fertility, tilth, and nutrient cycling.[171] The Australian Dung Beetle Project (1965–1985), introduced species of dung beetle to Australia from South Africa and Europe to reduce populations of *Musca vetustissima*, following successful trials of this technique in Hawaii.[170] The American Institute of Biological Sciences reports that dung beetles save the United States cattle industry an estimated US$380 million annually through burying above-ground livestock feces.[172]

The Dermestidae are often used in taxidermy and in the preparation of scientific specimens, to clean soft tissue from bones.[173] Larvae feed on and remove cartilage along with other soft tissue.[174][175]

As food and medicine

Mealworms in a bowl for human consumption

Beetles are the most widely eaten insects, with about 344 species used as food, usually at the larval stage.[176] The mealworm (the larva of the darkling beetle) and the rhinoceros beetle are among the species commonly eaten.[177] A wide range of species is also used in folk medicine to treat those suffering from a variety of disorders and illnesses, though this is done without clinical studies supporting the efficacy of such treatments.[178]

As biodiversity indicators

Due to their habitat specificity, many species of beetles have been suggested as suitable as indicators, their presence, numbers, or absence providing a measure of habitat quality. Predatory beetles such as the tiger beetles (Cicindelidae) have found scientific use as an indicator taxon for measuring regional patterns of biodiversity. They are suitable for this as their taxonomy is stable; their life history is well described; they are large and simple to observe when visiting a site; they occur around the world in many habitats, with species specialised to particular habitats; and their occurrence by species accurately indicates other species, both vertebrate and invertebrate.[179] According to the habitats, many other groups such as the rove beetles in human-modified habitats, dung beetles in savannas[180] and saproxylic beetles in forests[181] have been suggested as potential indicator species.[182]

In art and adornment

Zopheridae in jewellery at the Texas A&M University Insect Collection

Many beetles have beautiful and durable elytra that have been used as material in arts, with beetlewing the best example.[183] Sometimes, they are incorporated into ritual objects for their religious significance. Whole beetles, either as-is or encased in clear plastic, are made into objects ranging from cheap souvenirs such as key chains to expensive fine-art jewellery. In parts of Mexico, beetles of the genus *Zopherus* are made into living brooches by attaching costume jewelry and golden chains, which is made possible by the incredibly hard elytra and sedentary habits of the genus.[184]

In entertainment

Pendant watch in shape of beetle, Switzerland 1850-1900 gold, diamond, enamel

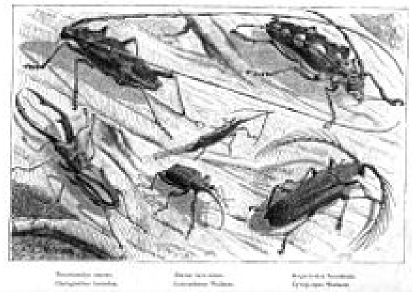
Fighting beetles are used for entertainment and gambling. This sport exploits the territorial behavior and mating competition of certain species of large beetles. In the Chiang Mai district of northern Thailand, male *Xylotrupes* rhinoceros beetles are caught in the wild and trained for fighting. Females are held inside a log to stimulate the fighting males with their pheromones.[185] These fights may be competitive and involve gambling both money and property.[186] In South Korea the Dytiscidae species *Cybister tripunctatus* is used in a roulette-like game.[187]

Beetles are sometimes used as instruments: the Onabasulu of Papua New Guinea historically used the weevil *Rhynchophorus ferrugineus* as a musical instrument by letting the human mouth serve as a variable resonance chamber for the wing vibrations of the live adult beetle.[186]

As pets

Some species of beetle are kept as pets, for example diving beetles (Dytiscidae) may be kept in a domestic fresh water tank.[188]

In Japan the practice of keeping horned rhinoceros beetles (Dynastinae) and stag beetles (Lucanidae) is particularly popular amongst young boys.[189] Such is the popularity in Japan that vending machines dispensing live beetles were developed in 1999, each holding up to 100 stag beetles.[190][191]



"Remarkable Beetles Found at Simunjon, Borneo".[c] A few of the 2000 species of beetle collected by Alfred Russel Wallace in Borneo

As things to collect

Beetle collecting became extremely popular in the Victorian era.[192] The naturalist Alfred Russel Wallace collected (by his own count) a total of 83,200 beetles during the eight years described in his 1869 book *The Malay Archipelago*, including 2,000 species new to science.[193]

As inspiration for technologies

Several coleopteran adaptations have attracted interest in biomimetics with possible commercial applications. The bombardier beetle's powerful repellent spray has inspired the development of a fine mist spray technology, claimed to have a low carbon impact compared to aerosol sprays.[194] Moisture harvesting behavior by the Namib desert beetle (*Stenocara gracilipes*) has inspired a self-filling water bottle which utilises hydrophilic and hydrophobic materials to benefit people living in dry regions with no regular rainfall.[195]

Living beetles have been used as cyborgs. A Defense Advanced Research Projects Agency funded project implanted electrodes into *Mecynorhina torquata* beetles, allowing them to be remotely controlled via a radio receiver held on its back, as proof-of-concept for surveillance work.[196] Similar technology has been applied to enable a human operator to control the free-flight steering and walking gaits of *Mecynorhina torquata* as well as graded turning and backward walking of *Zophobas morio*.[197][198][199]

In conservation

Since beetles form such a large part of the world's biodiversity, their conservation is important, and equally, loss of habitat and biodiversity is essentially certain to impact on beetles. Many species of beetles have very specific habitats and long life cycles that make them vulnerable. Some species are highly threatened while others are already feared extinct.[200] Island species tend to be more susceptible as in the case of *Helictopleurus undatus* of Madagascar which is thought to have gone extinct during the late 20th century.[201] Conservationists have attempted to arouse a liking for beetles with flagship species like the stag beetle, *Lucanus cervus*,[202] and tiger beetles (Cicindelidae). In Japan the Genji firefly, *Luciola cruciata*, is extremely popular, and in South Africa the Addo elephant dung beetle offers promise for broadening ecotourism beyond the big five tourist mammal species. Popular dislike of pest beetles, too, can be turned into public interest in insects, as can unusual ecological adaptations of species like the fairy shrimp hunting beetle, *Cicinis bruchi*.[203]

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Bed bug

Bed bugs are a type of insect that feed on human blood, usually at night.[7] Their bites can result in a number of health impacts including skin rashes, psychological effects and allergic symptoms.[5] Bed bug bites may lead to skin changes ranging from invisible to small areas of redness to prominent blisters.[1][2] Symptoms may take between minutes to days to appear and itchiness is generally present.[2] Some individuals may feel tired or have a fever.[2] Typically, uncovered areas of the body are affected and often three bites occur in a row.[2] Bed bugs bites are not known to transmit any infectious disease.[5][7] Complications may rarely include areas of dead skin or vasculitis.[2]

Bed bug bites are caused primarily by two species of insects of the *Cimex* type: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*, primarily in the tropics.[3] Their size ranges between 1 and 7 mm.[7] They spread by crawling between nearby locations or by being carried within personal items.[2] Infestation is rarely due to a lack of hygiene but is more common in high-density areas.[2][8] Diagnosis involves both finding the bugs and the occurrence of compatible symptoms.[5] Bed bugs spend much of their time in dark, hidden locations like mattress seams or cracks in the wall.[2]

Treatment is directed towards the symptoms.[2] Eliminating bed bugs from the home is often difficult, partly because bed bugs can survive up to a year without feeding.[2] Repeated treatments of a home may be required.[2] These treatments may include heating the room to 50 °C (122 °F) for more than 90 minutes, frequent vacuuming, washing clothing at high temperatures, and the use of various pesticides.[2]

Bed bugs occur in all regions of the globe.[7] Rates of infestations are relatively common, following an increase since the 1990s.[3][4][6] The exact causes of this increase are unclear; theories including increased human travel, more frequent exchange of second-hand furnishings, a greater focus on control of other pests, and increasing resistance to pesticides.[4] Bed bugs have been known human parasites for thousands of years.[2]

Bed bugs

Other names	Cimicosis, bed bug bites, bedbugs, bed bug infestation

An adult bed bug (*Cimex lectularius*) with the typical flattened oval shape

Specialty	Family medicine, dermatology
Symptoms	None to prominent blisters, itchy[1][2]
Usual onset	Minutes to days after the bite[2]
Causes	*Cimex* (primarily *Cimex lectularius* and *Cimex hemipterus*)[3]
Risk factors	Travel, second-hand furnishings[4]
Diagnostic method	Based on finding bed bugs and symptoms[5]
Differential diagnosis	Allergic reaction, scabies, dermatitis herpetiformis[2]
Treatment	Symptomatic, bed bug eradication[2]
Medication	Antihistamines, corticosteroids[2]
Frequency	Relatively common[6]

Contents

Signs and symptoms

Skin


Bedbug bites

Individual responses to bites vary, ranging from no visible effect (in about 20–70%),[3][5] to small macular spots, to prominent wheals and bullae formations along with intense itching that may last several days.[5] The bites often occur in a line. A central spot of bleeding may also occur due to the release of anticoagulants in the bug's saliva.[4]

Symptoms may not appear until some days after the bites have occurred.[5] Reactions often become more brisk after multiple bites due to possible sensitization to the salivary proteins of the bed bug.[3] The skin reaction usually occurs in the area of the bite which is most commonly the arms, shoulders and legs as they are more frequently exposed at night.[5] Numerous bites may lead to an erythematous rash or urticaria.[5]

Psychological

Serious infestations and chronic attacks can cause anxiety, stress, and insomnia.[5] Development of refractory delusional parasitosis is possible, as a person develops an overwhelming obsession with bed bugs.[9]

Other

A number of other symptoms may occur from either the bite of the bed bugs or from their exposure. Anaphylaxis from the injection of serum and other nonspecific proteins has been rarely documented.[5][10] Due to each bite taking a tiny amount of blood, chronic or severe infestation may lead to anemia.[5] Bacterial skin infection may occur due to skin break down from scratching.[5][11] Systemic poisoning may occur if the bites are numerous.[12] Exposure to bed bugs may trigger an asthma attack via the effects of airborne allergens although evidence of this association is limited.[5] There is no evidence that bed bugs transmit infectious diseases[5][7] even though they appear physically capable of carrying pathogens and this possibility has been investigated.[3][5] The bite itself may be painful thus resulting in poor sleep and worse work performance.[5]


Bedbug bites

Similar to humans, pets can also be bitten by bed bugs. The signs left by the bites are the same as in case of people and cause identical symptoms (skin irritation, scratching etc).

Insect

Bed bug infestations are primarily the result of two species of insects from genus *Cimex*: *Cimex lectularius* (the common bed bug) and *Cimex hemipterus*.[3] These insects feed exclusively on blood and may survive a year without eating.[3] Adult *Cimex* are light brown to reddish-brown, flat, oval, and have no hind wings. The front wings are vestigial and reduced to pad-like structures. Adults grow to 4–5 mm (0.16–0.20 in) long and 1.5–3 mm (0.059–0.118 in) wide.

An adult bed bug is about 4 to 5 mm long.

Bed bugs have five immature nymph life stages and a final sexually mature adult stage.[13] They shed their skins through ecdysis at each stage, discarding their outer exoskeleton.[14] Newly hatched nymphs are translucent, lighter in color, and become browner as they moult and reach maturity. Bed bugs may be mistaken for other insects, such as booklice, small cockroaches, or carpet beetles; however, when warm and active, their movements are more ant-like, and like most other true bugs, they emit a characteristic disagreeable odor when crushed.

Bed bugs are obligatory bloodsuckers. They have mouth parts that saw through the skin and inject saliva with anticoagulants and painkillers. Sensitivity of humans varies from extreme allergic reaction to no reaction at all (about 20%). The bite usually produces swelling with no red spot, but when many bugs feed on a small area, reddish spots may appear after the swelling subsides.[15] Bedbugs prefer exposed skin, preferably the face, neck, and arms of a sleeping person.

Bed bugs are attracted to their hosts primarily by carbon dioxide, secondarily by warmth, and also by certain chemicals.[4][16][17][18] *Cimex lectularius* only feeds every five to seven days, which suggests that it does not spend the majority of its life searching for a host. When a bed bug is starved, it leaves its shelter and searches for a host. It returns to its shelter after successful feeding or if it encounters exposure to light.[19] *Cimex lectularius* aggregate under all life stages and mating conditions. Bed bugs may choose to aggregate because of predation, resistance to desiccation, and more opportunities to find a mate. Airborne pheromones are responsible for aggregations.[20]

Spread

Infestation is rarely caused by a lack of hygiene.[8] Transfer to new places is usually in the personal items of the human they feed upon.[3] Dwellings can become infested with bed bugs in a variety of ways, such as:

- Bugs and eggs inadvertently brought in from other infested dwellings on a visiting person's clothing or luggage;
- Infested items (such as furniture especially beds or couches, clothing, or backpacks) brought in a home or business;
- Proximity of infested dwellings or items, if easy routes are available for travel, e.g. through ducts or false ceilings;
- Wild animals (such as bats or birds)[21][22] that may also harbour bed bugs or related species such as the bat bug;
- People visiting an infested area (e.g. dwelling, means of transport, entertainment venue, or lodging) and carrying the bugs to another area on their clothing, luggage, or bodies. Bedbugs are increasingly found in air travel.[23]

Though bed bugs will opportunistically feed on pets, they do not live or travel on the skin of their hosts, and pets are not believed to be a factor in their spread.[24]

Diagnosis

A definitive diagnosis of health effects due to bed bugs requires a search for and finding of the insect in the sleeping environment as symptoms are not sufficiently specific.[5] Bed bugs classically form a line of bites colloquially referred to as "breakfast, lunch, and dinner" and rarely feed in the armpit or behind the knee which may help differentiate it from other biting insects.[4] If the number in a house is large a pungent sweet odor may be described.[4] There are specially trained dogs that can detect this smell.[2]

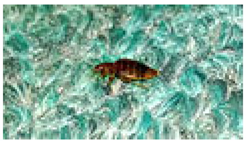
Detection

Bed bugs can exist singly, but tend to congregate once established. Although strictly parasitic, they spend only a tiny fraction of their lifecycles physically attached to hosts. Once a bed bug finishes feeding, it relocates to a place close to a known host, commonly in or near beds or couches in clusters of adults, juveniles, and eggs—which entomologists call harborage areas or simply harborages to which the insect returns after future feedings by following chemical trails. These places can vary greatly in format, including luggage, inside of vehicles, within furniture, among bedside clutter—even inside electrical sockets and nearby laptop computers. Bed bugs may also nest near animals that have nested within a dwelling, such as bats, birds,[22] or rodents. They are also capable of surviving on domestic cats and dogs, though humans are the preferred host of *C. lectularius*.[25]

Bed bugs can also be detected by their characteristic smell of rotting raspberries.[26] Bed bug detection dogs are trained to pinpoint infestations, with a possible accuracy rate between 11% and 83%.[6] Homemade detectors have been developed.[27][28]

Eggs and two adults found inside a dresser

Fecal spot



Bed bug on carpet

Differential diagnosis

Other possible conditions with which these conditions can be confused include scabies, gamasoidosis, allergic reactions, mosquito bites, spider bites, chicken pox and bacterial skin infections.[5]

Prevention

To prevent bringing home bed bugs, travelers are advised to take precautions after visiting an infested site: generally, these include checking shoes on leaving the site, changing clothes outside the house before entering, and putting the used clothes in a clothes dryer outside the house. When visiting a new lodging, it is advised to check the bed before taking suitcases into the sleeping area, and putting the suitcase on a raised stand to make bedbugs less likely to crawl in. An extreme measure would be putting the suitcase in the tub. Clothes should be hung up or left in the suitcase, and never left on the floor.[29] The founder of a company dedicated to bedbug extermination said that 5% of hotel rooms he books into were infested. He advised people never to sit down on public transport; check office chairs, plane seats, and hotel mattresses; and monitor and vacuum home beds once a month.[30]

Management

Treatment requires keeping the person from being repeatedly bitten and possible symptomatic use of antihistamines and corticosteroids (either topically or systemically).[5] There however is no evidence that medications improve outcomes and symptoms usually resolve without treatment in 1–2 weeks.[3][4]

Avoiding repeated bites can be difficult, since it usually requires eradicating bed bugs from a home or workplace; eradication frequently requires a combination of pesticide and non-pesticide approaches.[3] Pesticides that have historically been found to be effective include pyrethroids, dichlorvos and malathion.[4] Resistance to pesticides has increased significantly over time and there are concerns of negative health effects from their use.[3] Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses have been recommended.[3]

Once established, bed bugs are extremely difficult to get rid of.[3] This frequently requires a combination of nonpesticide approaches and the use of insecticides.[3][4]

Mechanical approaches, such as vacuuming up the insects and heat-treating or wrapping mattresses, are effective.[3][6] An hour at a temperature of 45 °C (113 °F) or over, or two hours at less than −17 °C (1 °F) kills them.[6] This may include a domestic clothes drier for fabric or a commercial steamer. Bed bugs and their eggs will die on contact when exposed to surface temperatures above 180 °F (82 °C) and a steamer can reach well above 230 °F (110 °C).[15][31] A study found 100% mortality rates for bed bugs exposed to temperatures greater than 50 °C (122 °F) for more than 2 minutes. The study recommended maintaining temperatures of above 48 °C (118 °F) for more than 20 min to effectively kill all life stages of bed bugs, and because in practice treatment times of 6 to 8 hours are used to account for cracks and indoor clutter.[32] This method is expensive and has caused fires.[6][15] Starving bedbugs is not effective, as they can survive without eating for 100 to 300 days, depending on temperature.[6]

It was stated in 2012 that no truly effective insecticides were available.[6] Insecticides that have historically been found effective include pyrethroids, dichlorvos, and malathion.[4] Resistance to pesticides has increased significantly in recent decades, and harm to health from their use is of concern.[3] The carbamate insecticide propoxur is highly toxic to bed bugs, but it has potential toxicity to children exposed to it, and the US Environmental Protection Agency has been reluctant to approve it for indoor use.[33] Boric acid, occasionally applied as a safe indoor insecticide, is not effective against bed bugs[34] because they do not groom.[35]

Epidemiology

Bed bugs occur around the world.[36] Before the 1950s about 30% of houses in the United States had bedbugs.[2] Rates of infestation in developed countries, while decreasing from the 1930s to the 1980s, have increased dramatically since the 1980s.[3][4][36] This is believed to be partly due to the use of DDT to kill cockroaches.[37] The invention of the vacuum cleaner and simplification of furniture design may have also played a role.[37] Others believe it might simply be the cyclical nature of the organism.[38]

The dramatic increase in bedbug populations in the developed world, which began in the 1980s, is thought to be due to greater foreign travel, increased immigration from the developing world to the developed world, more frequent exchange of second-hand furnishings among homes, a greater focus on control of other pests, resulting in neglect of bed bug countermeasures, and increasing bedbug resistance to pesticides.[4][39] Lower cockroach populations due to insecticide use may have aided bed bugs' resurgence, since cockroaches are known to sometimes predate them.[40] Bans on DDT and other potent pesticides may have also contributed.[41][42]

The U.S. National Pest Management Association reported a 71% increase in bed bug calls between 2000 and 2005.[43] The number of reported incidents in New York City alone rose from 500 in 2004 to 10,000 in 2009.[44] In 2013, Chicago was listed as the number 1 city in the United States for bedbug infestations.[45] As a result, the Chicago City Council passed a bed bug control ordinance to limit their spread. Additionally, bed bugs are reaching places in which they never established before, such as southern South America.[46][47]

The rise in infestations has been hard to track because bed bugs are not an easily identifiable problem and is one that people prefer not to discuss. Most of the reports are collected from pest-control companies, local authorities, and hotel chains.[48] Therefore, the problem may be more severe than is currently believed.[49]

Species

The common bed bug (*C. lectularius*) is the species best adapted to human environments. It is found in temperate climates throughout the world. Other species include *Cimex hemipterus*, found in tropical regions, which also infests poultry and bats, and *Leptocimex boueti*, found in the tropics of West Africa and South America, which infests bats and humans. *Cimex pilosellus* and *Cimex pipistrella* primarily infest bats, while *Haematosiphon inodora*, a species of North America, primarily infests poultry.[50]

History

Cimicidae the ancestor of modern bed bugs first emerged approximately 115 million years ago, more than 30 million years before bats, their previously presumed initial host first appeared. From unknown ancestral hosts, a variety of different lineages evolved which specialized in either bats or birds. The common (*C. lectularius*) and tropical bed bug (*C. hemipterus*), split 40 million years before *Homo* evolution. Humans became hosts to bed bugs through host specialist extension (rather than switching) on three separate occasions.[51][52]

Bed bugs were mentioned in ancient Greece as early as 400 BC, and were later mentioned by Aristotle. Pliny's *Natural History*, first published *circa* AD 77 in Rome, claimed bed bugs had medicinal value in treating ailments such as snake bites and ear infections. Belief in the medicinal use of bed bugs persisted until at least the 18th century, when Guettard recommended their use in the treatment of hysteria.[53]

Bed bugs were first mentioned in Germany in the 11th century, in France in the 13th century, and in England in 1583,[54] though they remained rare in England until 1670. Some in the 18th century believed bed bugs had been brought to London with supplies of wood to rebuild the city after the Great Fire of London (1666). Giovanni Antonio Scopoli noted their presence in Carniola (roughly equivalent to present-day Slovenia) in the 18th century.[55][56]

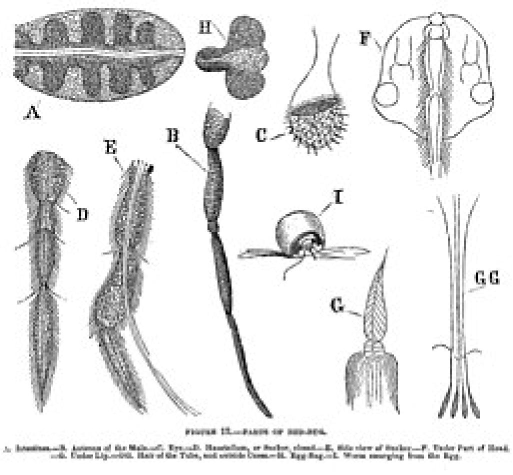
Traditional methods of repelling and/or killing bed bugs include the use of plants, fungi, and insects (or their extracts), such as black pepper;[57] black cohosh (*Actaea racemosa*); *Pseudarthria hookeri*; *Laggera alata* (Chinese *yángmáo cǎo* | 羊毛草);[15] *Eucalyptus saligna* oil;[58][59] henna (*Lawsonia inermis* or camphire);[60] "infused oil of *Melolontha vulgaris*" (presumably cockchafer); fly agaric (*Amanita muscaria*); tobacco; "heated oil of Terebinthina" (i.e. true turpentine); wild mint (*Mentha arvensis*); narrow-leaved pepperwort (*Lepidium ruderale*); *Myrica* spp. (e.g. bayberry); Robert geranium (*Geranium robertianum*); bugbane (*Cimicifuga* spp.); "herb and seeds of *Cannabis*"; "opulus" berries (possibly maple or European cranberrybush); masked hunter bugs (*Reduvius personatus*), "and many others".[61]

1870s–1890s advertisement for a bed bug exterminator. It reads "Use Getz cockroach and bed bug exterminators, sold by all druggists."

In the mid-19th century, smoke from peat fires was recommended as an indoor domestic fumigant against bed bugs.[62]

Dusts have been used to ward off insects from grain storage for centuries, including plant ash, lime, dolomite, certain types of soil, and diatomaceous earth or Kieselguhr.[63] Of these, diatomaceous earth in particular has seen a revival as a nontoxic (when in amorphous form) residual pesticide for bed bug abatement. While diatomaceous earth often performs poorly, silica gel may be effective.[64][65]

Basket-work panels were put around beds and shaken out in the morning in the UK and in France in the 19th century. Scattering leaves of plants with microscopic hooked hairs around a bed at night, then sweeping them up in the morning and burning them, was a technique reportedly used in Southern Rhodesia and in the Balkans.[66]



1860 engraving of bed bug parts: *A*. Intestines – *B*. Antenna of the male – *C*. Eye – *D*. Haustellum, or sucker, closed – *E*. Side view of sucker – *F*. Under part of head – *G*. Under lip – *GG*. Hair of the tube, and outside cases – *H*. Egg-bag – *I*. Larva emerging from the eggs

Bean leaves have been used historically to trap bedbugs in houses in Eastern Europe. The trichomes on the bean leaves capture the insects by impaling the feet (tarsi) of the insects. The leaves are then destroyed.[67]

20th century

Before the mid-20th century, bed bugs were very common. According to a report by the UK Ministry of Health, in 1933, all the houses in many areas had some degree of bed bug infestation.[48] The increase in bed bug populations in the early 20th century has been attributed to the advent of electric heating, which allowed bed bugs to thrive year-round instead of only in warm weather.[68]

Bed bugs were a serious problem at US military bases during World War II.[69] Initially, the problem was solved by fumigation, using Zyklon Discoids that released hydrogen cyanide gas, a rather dangerous procedure.[69] Later, DDT was used to good effect.[69]

The decline of bed bug populations in the 20th century is often credited to potent pesticides that had not previously been widely available.[70] Other contributing factors that are less frequently mentioned in news reports are increased public awareness and slum clearance programs that combined pesticide use with steam disinfection, relocation of slum dwellers to new housing, and in

some cases also follow-up inspections for several months after relocated tenants moved into their new housing.[68]

Society and culture

Legal action

Bed bugs are an increasing cause for litigation.[71] Courts have, in some cases, exacted large punitive damage judgments on some hotels.[72][73][74] Many of New York City's Upper East Side homeowners have been afflicted, but they tend to remain publicly silent in order not to ruin their property values and be seen as suffering a blight typically associated with the lower classes.[75] Local Law 69 in New York City requires owners of buildings with three or more units to provide their tenants and potential tenants with reports of bedbug history in each unit. They must also prominently post these listings and reports in their building.[76]

Literature

- "Good night, sleep tight, don't let the bed bugs bite," is a traditional saying.[77]
- *The Bedbug* (Russian: Клоп, Klop) is a play by Vladimir Mayakovsky written in 1928–1929.

Research

Bed bug secretions can inhibit the growth of some bacteria and fungi; antibacterial components from the bed bug could be used against human pathogens, and be a source of pharmacologically active molecules as a resource for the discovery of new drugs.[78]

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Moth

Moths are a polyphyletic group of insects that includes all members of the order Lepidoptera that are not butterflies, with moths making up the vast majority of the order. There are thought to be approximately 160,000 species of moth,[1] many of which have yet to be described. Most species of moth are nocturnal, but there are also crepuscular and diurnal species.

Moths	
	
Emperor gum moth, *Opodiphthera eucalypti*	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
(unranked):	Heterocera

Contents

Differences between butterflies and moths

While the butterflies form a monophyletic group, the moths, comprising the rest of the Lepidoptera, do not. Many attempts have been made to group the superfamilies of the Lepidoptera into natural groups, most of which fail because one of the two groups is not monophyletic: Microlepidoptera and Macrolepidoptera, Heterocera and Rhopalocera, Jugatae and Frenatae, Monotrysia and Ditrysia.[2]

Although the rules for distinguishing moths from butterflies are not well established, one very good guiding principle is that butterflies have thin antennae and (with the exception of the family Hedylidae) have small balls or clubs at the end of their antennae. Moth antennae are usually feathery with no ball on the end. The divisions are named by this principle: "club-antennae" (Rhopalocera) or "varied-antennae" (Heterocera).

Etymology

The modern English word "moth" comes from Old English "*moððe*" (cf. Northumbrian "*mohðe*") from Common Germanic (compare Old Norse "*motti*", Dutch "*mot*", and German "*Motte*" all meaning "moth"). Its origins are possibly related to the Old English "*maða*" meaning "maggot" or from the root of "midge" which until the 16th century was used mostly to indicate the larva, usually in reference to devouring clothes.

Caterpillar

Poplar hawk-moth caterpillar (*Laothoe populi*)

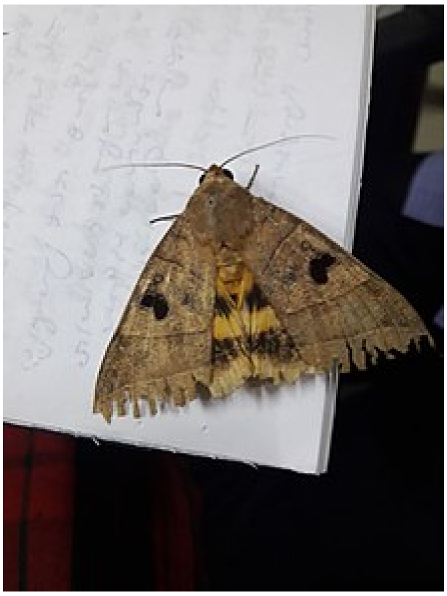
Moth larvae, or caterpillars, make cocoons from which they emerge as fully grown moths with wings. Some moth caterpillars dig holes in the ground, where they live until they are ready to turn into adult moths.[3]

History

Moth larva from India

Moths evolved long before butterflies, with fossils having been found that may be 190 million years old. Both types of Lepidoptera are thought to have evolved along with flowering plants, mainly because most modern species feed on flowering plants, both as adults and larvae. One of the earliest species thought to be a moth-ancestor is *Archaeolepis mane*, whose fossil fragments show scaled wings similar to caddisflies in their veining.[4]

Economics



Moth from Kerala, India

Significance to humans

Some moths, particularly their caterpillars, can be major agricultural pests in many parts of the world. Examples include corn borers and bollworms.[5] The caterpillar of the gypsy moth (*Lymantria dispar*) causes severe damage to forests in the northeastern United States, where it is an invasive species. In temperate climates, the codling moth causes extensive damage, especially to fruit farms. In tropical and subtropical climates, the diamondback moth (*Plutella xylostella*) is perhaps the most serious pest of brassicaceous crops. Also in sub-Saharan Africa, the African sugarcane borer is a major pest of sugarcane, maize, and sorghum.[6]

Several moths in the family Tineidae are commonly regarded as pests because their larvae eat fabric such as clothes and blankets made from natural proteinaceous fibers such as wool or silk.[7] They are less likely to eat mixed materials containing some artificial fibers. There are some reports that they may be repelled by the scent of wood from juniper and cedar, by lavender, or by other natural oils; however, many consider this unlikely to prevent infestation. Naphthalene (the chemical used in mothballs) is considered more effective, but there are concerns over its effects on human health.

Moth larvae may be killed by freezing the items which they infest for several days at a temperature below −8 °C (18 °F).[8]

Despite being notorious for eating clothing, most moth adults do not eat at all. Many, like the Luna, Polyphemus, Atlas, Promethea, cecropia, and other large moths do not have mouth parts. While there are many species of adult moths that do eat, there are many that will drink nectar.[7]

Some moths are farmed for their economic value. The most notable of these is the silkworm, the larva of the domesticated moth *Bombyx mori*. It is farmed for the silk with which it builds its cocoon. As of 2002, the silk industry produces more than 130 million kilograms of raw silk, worth about 250 million U.S. dollars, each year.[9][10][11]

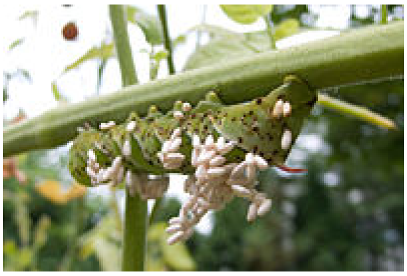
Not all silk is produced by *Bombyx mori*. There are several species of Saturniidae that also are farmed for their silk, such as the ailanthus moth (*Samia cynthia* group of species), the Chinese oak silkmoth (*Antheraea pernyi*), the Assam silkmoth (*Antheraea assamensis*), and the Japanese silk moth (*Antheraea yamamai*).

An adult male pine processionary moth (*Thaumetopoea pityocampa*). This species is a serious forest pest when in its larval state. Notice the bristle springing from the underside of the hindwing (frenulum) and running forward to be held in a small catch of the forewing, whose function is to link the wings together.

The larvae of many species are used as food, particularly in Africa, where they are an important source of nutrition. The mopane worm, the caterpillar of *Gonimbrasia belina*, from the family Saturniidae, is a significant food resource in southern Africa. Another saturniid used as food is the cavorting emperor (*Usta terpsichore*). In one country alone, Congo, more than 30 species of moth larvae are harvested. Some are sold not only in the local village markets, but are shipped by the ton from one country to another.[12]

Predators and parasites

Nocturnal insectivores often feed on moths; these include some bats, some species of owls and other species of birds. Moths also are eaten by some species of lizards, amphibians, cats, dogs, rodents, and some bears. Moth larvae are vulnerable to being parasitized by Ichneumonidae.



Tomato hornworm parasitized by braconid wasps

Baculoviruses are parasite double-stranded DNA insect viruses that are used mostly as biological control agents. They are members of the Baculoviridae, a family that is restricted to insects. Most baculovirus isolates have been obtained from insects, in particular from Lepidoptera.

There is evidence that ultrasound in the range emitted by bats causes flying moths to make evasive maneuvers because bats eat moths. Ultrasonic frequencies trigger a reflex action in the noctuid moth that causes it to drop a few inches in its flight to evade attack.[13] Tiger moths also emit clicks which can foil bats' echolocation.[14][15]

The fungus *Ophiocordyceps sinensis* infects the larvae of many different species of moths.[16]

Ecological importance

Some studies indicate that certain species of moths, such as those belonging to the families Erebidae and Sphingidae, may be the key pollinators for some flowering plants in the Himalayan ecosystem.[17][18]

Attraction to light

Moths frequently appear to circle artificial lights, although the reason for this behavior (positive phototaxis) remains unknown. One hypothesis is called celestial or transverse orientation. By maintaining a constant angular relationship to a bright celestial light, such as the moon, they can fly in a straight line. Celestial objects are so far away that, even after travelling great distances, the change in angle between the moth and the light source is negligible; further, the moon will always be in the upper part of the visual field, or on the horizon. When a moth encounters a much closer artificial light and uses it for navigation, the angle changes noticeably after only a short distance, in addition to being often below the horizon. The moth instinctively attempts to correct by turning toward the light, thereby causing airborne moths to come plummeting downward, and resulting in a spiral flight path that gets closer and closer to the light source.[19]

Studies have found that light pollution caused by increasing use of artificial lights has either led to a severe decline in moth population in some parts of the world[20][21][22] or has severely disrupted nocturnal pollination.[23][24]

Assorted moths in the University of Texas Insect Collection

Noteworthy moths

- Atlas moth (*Attacus atlas*), the largest moth in the world
- White witch moth (*Thysania agrippina*), the Lepidopteran with the longest wingspan
- Madagascan sunset moth (*Chrysiridia rhipheus*), considered to be one of the most impressive and beautiful Lepidoptera[25]
- Death's-head hawkmoth (*Acherontia* spp.), is associated with the supernatural and evil and has been featured in art and movies
- Peppered moth (*Biston betularia*), the subject of a well-known study in natural selection
- Luna moth (*Actias luna*)
- Grease moth (*Aglossa cuprina*), known to have fed on the rendered fat of humans[26]
- Emperor gum moth (*Opodiphthera eucalypti*)
- Polyphemus moth (*Antheraea polyphemus*)
- Bogong moth (*Agrotis infusa*), known to have been a food source for southeastern indigenous Australians
- Ornate moth (*Utetheisa ornatrix*), the subject of numerous behavioral studies regarding sexual selection

Moths of economic significance

- Gypsy moth (*Lymantria dispar*), an invasive species pest of hardwood trees in North America
- Winter moth (*Operophtera brumata*), an invasive species pest of hardwood trees, cranberry and blueberry in northeastern North America
- Corn earworm or cotton bollworm (*Helicoverpa zea*), a major agricultural pest
- Indianmeal moth (*Plodia interpunctella*), a major pest of grain and flour
- Codling moth (*Cydia pomonella*), a pest mostly of apple, pear and walnut trees
- Light brown apple moth (*Epiphyas postvittana*), a highly polyphagous pest
- Silkworm (*Bombyx mori*), for its silk
- Wax moths (*Galleria mellonella*, *Achroia grisella*), pests of bee hives
- *Duponchelia fovealis*, a new invasive pest of vegetables and ornamental plants in the United States

Gallery

Diagram of a plume moth from Robert Hooke's *Micrographia*

Leaf-shaped moth (*Pergesa acteus*)

Giant grey moth (*Agrius convolvuli*)

Oleander hawk-moth or army green moth (*Daphnis nerii*)

Six-spot burnet moths mating (*Zygaena filipendulae*)

Protective silk (or similar material) case (cocoon)

A caterpillar of death's-head hawkmoth

Mating pair of *Laothoe populi*, or poplar hawkmoths, showing two different color variants

White-lined sphinx moth in Colorado, United States

Closeup of a common clothes moth

Giant silk moth (*Adelowalkeria tristygma*)

Adult emperor moth (*Gonimbrasia belina*)

Sphingidae - Kerala

See also

- Baculovirus
- Butterfly
- Clothing moth
- Comparison of butterflies and moths
- Lepidoptera
- List of moths
- Lepidopterism
- Pollination

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4. Chihuahuan Desert Nature Center
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Studying the evolution of butterflies and moths is challenging, since fossils are so rare. But the few Lepidopteran fossils that exist, captured in amber or compressed in fine-grained rocks, show great detail. The earliest Lepidopteran fossils appear in rocks that are about 190 million years old. These tiny fragments of scaled wings and bodies clearly indicate that moths evolved before butterflies.

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Ant

Ants are eusocial insects of the family **Formicidae** and, along with the related wasps and bees, belong to the order Hymenoptera. Ants evolved from wasp-like ancestors in the Cretaceous period, about 140 million years ago, and diversified after the rise of flowering plants. More than 12,500 of an estimated total of 22,000 species have been classified.[5][6] They are easily identified by their elbowed antennae and the distinctive node-like structure that forms their slender waists.

Ants form colonies that range in size from a few dozen predatory individuals living in small natural cavities to highly organised colonies that may occupy large territories and consist of millions of individuals. Larger colonies consist of various castes of sterile, wingless females, most of which are workers (ergates), as well as soldiers (dinergates) and other specialised groups.[7][8] Nearly all ant colonies also have some fertile males called "drones" (aner) and one or more fertile females called "queens" (gynes).[8] The colonies are described as superorganisms because the ants appear to operate as a unified entity, collectively working together to support the colony.[9][10]

Ants have colonised almost every landmass on Earth. The only places lacking indigenous ants are Antarctica and a few remote or inhospitable islands. Ants thrive in most ecosystems and may form 15–25% of the terrestrial animal biomass.[11] Their success in so many environments has been attributed to their social organisation and their ability to modify habitats, tap resources, and defend themselves. Their long co-evolution with other species has led to mimetic, commensal, parasitic, and mutualistic relationships.[12]

Ant societies have division of labour, communication between individuals, and an ability to solve complex problems.[13] These parallels with human societies have long been an inspiration and subject of study. Many human cultures make use of ants in cuisine, medication, and rituals. Some species are valued in their role as biological pest control agents.[14] Their ability to exploit resources may bring ants into conflict with humans, however, as they can damage crops and invade buildings. Some species, such as the red imported fire ant (*Solenopsis invicta*), are regarded as invasive species, establishing themselves in areas where they have been introduced accidentally.[15]

Ants

Temporal range: 140–0 Ma[1]

PreЄ Є O S D C P T J K PgN

Berriasian – Present

A group of fire ants.

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hymenoptera
Superfamily:	Formicoidea
Family:	Formicidae Latreille, 1809

Type species

Formica rufa

Linnaeus, 1761

Subfamilies

Contents

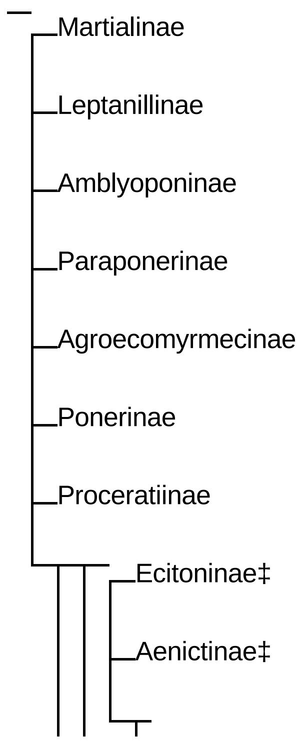
Etymology

The word *ant* and its chiefly dialectal form *emmet*[16] come from *ante*, *emete* of Middle English, which come from *ǣmette* of Old English, and these are all related to the dialectal Dutch *emt* and the Old High German *āmeiza*, from which comes the modern German *Ameise*. All of these words come from West Germanic **ǣmaitjōn*, and the original meaning of the word was "the biter" (from Proto-Germanic **ai-*, "off, away" + **mait-* "cut").[17][18] The family name Formicidae is derived from the Latin *formīca* ("ant")[19] from which the words in other Romance languages, such as the Portuguese *formiga*, Italian *formica*, Spanish *hormiga*, Romanian *furnică*, and French *fourmi* are derived. It has been hypothesised that a Proto-Indo-European word *morwi- was used, cf. Sanskrit vamrah, Latin formīca, Greek μύρμηξ *mýrmēx*, Old Church Slavonic *mravìji*, Old Irish *moirb*, Old Norse *maurr*, Dutch *mier*.[20]

Taxonomy and evolution

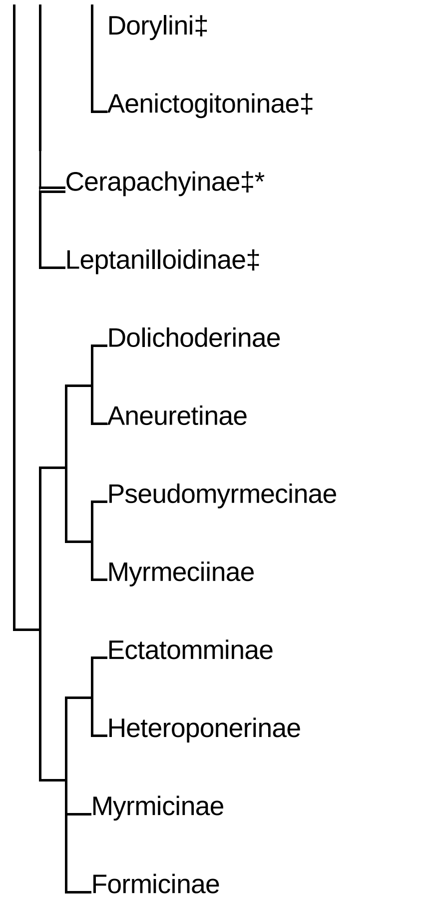
- Agroecomyrmecinae
- Amblyoponinae (incl. "Apomyrminae")
- Aneuretinae
- †Brownimeciinae
- Dolichoderinae
- Dorylinae
- Ectatomminae
- †Formiciinae
- Formicinae
- Heteroponerinae
- Leptanillinae
- Martialinae
- Myrmeciinae (incl. "Nothomyrmeciinae")
- Myrmicinae
- Paraponerinae
- Ponerinae
- Proceratiinae
- Pseudomyrmecinae
- †Sphecomyrminae

Cladogram of subfamilies



The family Formicidae belongs to the order Hymenoptera, which also includes sawflies, bees, and wasps. Ants evolved from a lineage within the stinging wasps, and a 2013 study suggests that they are a sister group of the Apoidea.[21] In 1966, E. O. Wilson and his colleagues identified the fossil remains of an ant (*Sphecomyrma*) that lived in the Cretaceous period. The specimen, trapped in amber dating back to around 92 million years ago, has features found in some wasps, but not found in modern ants.[22] *Sphecomyrma* was possibly a ground forager, while *Haidomyrmex* and *Haidomyrmodes*, related genera in subfamily Sphecomyrminae, are reconstructed as active arboreal predators.[23] Older ants in the genus *Sphecomyrmodes* have been found in 99 million year-old amber from Myanmar.[24][25] A 2006 study suggested that ants arose tens of millions of years earlier than previously thought, up to 168 million years ago.[1] After the rise of flowering plants about 100 million years ago they diversified and assumed ecological dominance around 60 million years ago.[26][1][27][28] Some groups, such as the Leptanillinae and Martialinae, are suggested to have diversified from early primitive ants that were likely to have been predators underneath the surface of the soil.[3][29]

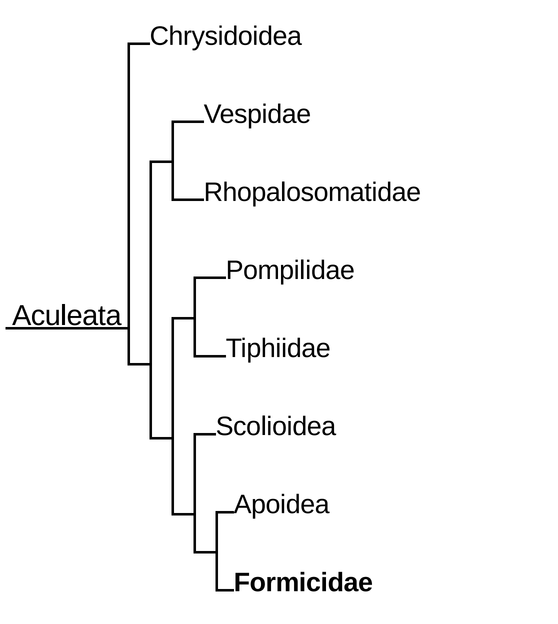
During the Cretaceous period, a few species of primitive ants ranged widely on the Laurasian supercontinent (the Northern Hemisphere). They were scarce in comparison to the populations of other insects, representing only about 1% of the entire insect population. Ants became dominant after adaptive radiation at the beginning of the Paleogene period. By the Oligocene and Miocene, ants had come to represent 20–40% of all insects found in major fossil deposits. Of the species that lived in the Eocene epoch, around one in 10 genera survive to the present. Genera surviving today comprise 56% of the genera in Baltic amber fossils (early Oligocene), and 92% of the genera in Dominican amber fossils (apparently early Miocene).[26][30]



A phylogeny of the extant ant subfamilies.[2][3]

*Cerapachyinae is paraphyletic

‡ The previous dorylomorph subfamilies were synonymized under Dorylinae by Brady *et al.* in 2014[4]



Phylogenetic position of the Formicidae.[21]

Play media

(video) Ants gathering food

Termites live in colonies and are sometimes called ‘white ants’, but termites are not ants. They are the sub-order Isoptera, and together with cockroaches they form the order Blattodea. Blattodeans are related to mantids, crickets, and other winged insects that do not undergo full metamorphosis. Like ants, termites are eusocial, with sterile workers, but they differ greatly in the genetics of reproduction. The similarity of their social structure to that of ants is attributed to convergent evolution.[31] Velvet ants look like large ants, but are wingless female wasps.[32][33]

Distribution and diversity

Region	Number of species [34]
Neotropics	2,162
Nearctic	580
Europe	180
Africa	2,500
Asia	2,080
Melanesia	275
Australia	985
Polynesia	42

Ants fossilised in Baltic amber

Ants are found on all continents except Antarctica, and only a few large islands, such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species.[35][36] Ants occupy a wide range of ecological niches and exploit many different food resources as direct or indirect herbivores, predators and scavengers. Most ant species are omnivorous generalists, but a few are specialist feeders. Their ecological dominance is demonstrated by their biomass: ants are estimated to contribute 15–20 % (on average and nearly 25% in the tropics) of terrestrial animal biomass, exceeding that of the vertebrates.[11]

Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in),[37][38] the largest species being the fossil *Titanomyrma giganteum*, the queen of which was 6 centimetres (2.4 in) long with a wingspan of 15 centimetres (5.9 in).[39] Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 12,000 species are currently known (with upper estimates of the potential existence of about 22,000) (see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants. Online databases of ant species, including AntBase (http://antbase.org/) and the Hymenoptera Name Server (https://hns.osu.edu/), help to keep track of the known and newly described species.[40] The relative ease with which ants may be sampled and studied in ecosystems has made them useful as indicator species in biodiversity studies.[41][42]

Morphology

Ants are distinct in their morphology from other insects in having elbowed antennae, metapleural glands, and a strong constriction of their second abdominal segment into a node-like petiole. The head, mesosoma, and metasoma are the three distinct body segments (formally tagmata). The petiole forms a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole may be formed by one or two nodes (the second alone, or the second and third abdominal segments).[43]

Like other insects, ants have an exoskeleton, an external covering that provides a protective casing around the body and a point of attachment for muscles, in contrast to the internal skeletons of humans and other vertebrates. Insects do not have lungs; oxygen and other gases, such as carbon dioxide, pass through their exoskeleton via tiny valves called spiracles. Insects also lack closed blood vessels; instead, they have a long, thin, perforated tube along the top of the body (called the "dorsal aorta") that functions like a heart, and pumps haemolymph toward the head, thus driving the circulation of the internal fluids. The nervous system consists of a ventral nerve cord that runs the length of the body, with several ganglia and branches along the way reaching into the extremities of the appendages.[44]

Head

An ant's head contains many sensory organs. Like most insects, ants have compound eyes made from numerous tiny lenses attached together. Ant eyes are good for acute movement detection, but do not offer a high resolution image. They also have three small ocelli (simple eyes) on the top of the head that detect light levels and polarization.[45] Compared to vertebrates, most ants have poor-to-mediocre eyesight and a few subterranean species are completely blind. However, some ants, such as Australia's

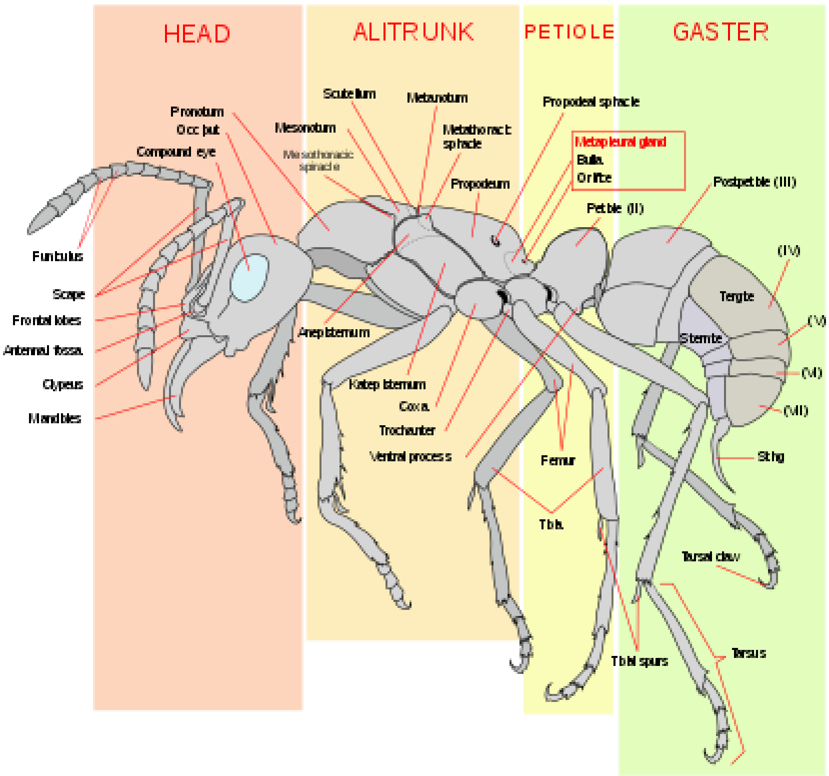


Diagram of a worker ant (*Pachycondyla verenae*)

bulldog ant, have excellent vision and are capable of discriminating the distance and size of objects moving nearly a metre away.[46]

Two antennae ("feelers") are attached to the head; these organs detect chemicals, air currents, and vibrations; they also are used to transmit and receive signals through touch. The head has two strong jaws, the mandibles, used to carry food, manipulate objects, construct nests, and for defence.[44] In some species, a small pocket (infrabuccal chamber) inside the mouth stores food, so it may be passed to other ants or their larvae.[47]

Mesosoma

Both the legs and wings of the ant are attached to the mesosoma ("thorax"). The legs terminate in a hooked claw which allows them to hook on and climb surfaces.[48] Only reproductive ants, queens, and males, have wings. Queens shed their wings after the nuptial flight, leaving visible stubs, a distinguishing feature of queens. In a few species, wingless queens (ergatoids) and males occur.[44]

Macro portrait of an ant

Metasoma

The metasoma (the "abdomen") of the ant houses important internal organs, including those of the reproductive, respiratory (tracheae), and excretory systems. Workers of many species have their egg-laying structures modified into stings that are used for subduing prey and defending their nests.[44]

Bull ant showing the powerful mandibles and the relatively large compound eyes that provide excellent vision

Polymorphism

In the colonies of a few ant species, there are physical castes—workers in distinct size-classes, called minor, median, and major ergates. Often, the larger ants have disproportionately larger heads, and correspondingly stronger mandibles. These are known as macrergates while smaller workers are known as micrergates.[8] Although formally known as dinergates, such individuals are sometimes called "soldier" ants because their stronger mandibles make them more effective in fighting, although they still are workers and their "duties" typically do not vary greatly from the minor or median workers. In a few species, the median workers are absent, creating a sharp divide between the minors and majors.[49] Weaver ants, for example,

have a distinct bimodal size distribution.[50][51] Some other species show continuous variation in the size of workers. The smallest and largest workers in *Pheidologeton diversus* show nearly a 500-fold difference in their dry-weights.[52]

Seven leafcutter ant workers of various castes (left) and two queens (right)

Workers cannot mate; however, because of the haplodiploid sex-determination system in ants, workers of a number of species can lay unfertilised eggs that become fully fertile, haploid males. The role of workers may change with their age and in some species, such as honeypot ants, young workers are fed until their gasters are distended, and act as living food storage vessels. These food storage workers are called *repletes*.[53] For instance, these replete workers develop in the North American honeypot ant *Myrmecocystus mexicanus*. Usually the largest workers in the colony develop into repletes; and, if repletes are removed from the colony, other workers become repletes, demonstrating the flexibility of this particular polymorphism.[54] This polymorphism in morphology and behaviour of workers initially was thought to be determined by environmental factors such as nutrition and hormones that led to different developmental paths; however, genetic differences between worker castes have been noted in *Acromyrmex* sp.[55] These polymorphisms are caused by relatively small genetic changes; differences in a single gene of *Solenopsis invicta* can decide whether the colony will have single or multiple queens.[56] The Australian jack jumper ant (*Myrmecia pilosula*) has only a single pair of chromosomes (with the males having just one chromosome as they are haploid), the lowest number known for any animal, making it an interesting subject for studies in the genetics and developmental biology of social insects.[57][58]

Life cycle

Meat eater ant nest during swarming

The life of an ant starts from an egg. If the egg is fertilised, the progeny will be female diploid; if not, it will be male haploid. Ants develop by complete metamorphosis with the larva stages passing through a pupal stage before emerging as an adult. The larva is largely immobile and is fed and cared for by workers. Food is given to the larvae by trophallaxis, a process in which an ant regurgitates liquid food held in its crop. This is also how adults share food, stored in the "social stomach". Larvae, especially in the later stages, may also be provided solid food, such as trophic eggs, pieces of prey, and seeds brought by workers.

The larvae grow through a series of four or five moults and enter the pupal stage. The pupa has the appendages free and not fused to the body as in a butterfly pupa.[59] The differentiation into queens and workers (which are both female), and different castes of workers, is influenced in some species by the nutrition the larvae obtain. Genetic influences and the control of gene expression by the developmental environment are complex and the determination of caste continues to be a subject of research.[60] Winged male ants, called drones, emerge from pupae along with the usually winged breeding females. Some species, such as army ants, have wingless queens. Larvae and pupae need to be kept at fairly constant temperatures to ensure proper development, and so often, are moved around among the various brood chambers within the colony.[61]

A new ergate spends the first few days of its adult life caring for the queen and young. She then graduates to digging and other nest work, and later to defending the nest and foraging. These changes are sometimes fairly sudden, and define what are called temporal castes. An explanation for the sequence is suggested by the high casualties involved in foraging, making it an acceptable risk only for ants who are older and are likely to die soon of natural causes.[62][63]

Ant colonies can be long-lived. The queens can live for up to 30 years, and workers live from 1 to 3 years. Males, however, are more transitory, being quite short-lived and surviving for only a few weeks.[64] Ant queens are estimated to live 100 times as long as solitary insects of a similar size.[65]

Ants are active all year long in the tropics, but, in cooler regions, they survive the winter in a state of dormancy known as hibernation. The forms of inactivity are varied and some temperate species have larvae going into the inactive state (diapause), while in others, the adults alone pass the winter in a state of reduced activity.[66]

Reproduction

Alate male ant, *Prenolepis imparis*

A wide range of reproductive strategies have been noted in ant species. Females of many species are known to be capable of reproducing asexually through thelytokous parthenogenesis.[67] Secretions from the male accessory glands in some species can plug the female genital opening and prevent females from re-mating.[68] Most ant species have a system in which only the queen and breeding females have the ability to mate. Contrary to popular belief, some ant nests have multiple queens, while others may exist without queens. Workers with the ability to reproduce are called "gamergates" and colonies that lack queens are then called gamergate colonies; colonies with queens are said to be queen-right.[69]

Ants mating

Drones can also mate with existing queens by entering a foreign colony. When the drone is initially attacked by the workers, it releases a mating pheromone. If recognized as a mate, it will be carried to the queen to mate.[70] Males may also patrol the nest and fight others by grabbing them with their mandibles, piercing their exoskeleton and then marking them with a pheromone. The marked male is interpreted as an invader by worker ants and is killed.[71]

Fertilised meat-eater ant queen beginning to dig a new colony

Most ants are univoltine, producing a new generation each year.[72] During the species-specific breeding period, winged females and winged males, known to entomologists as alates, leave the colony in what is called a nuptial flight. The nuptial flight usually takes place in the late spring or early summer when the weather is hot and humid. Heat makes flying easier and freshly fallen rain makes the ground softer for mated queens to dig nests.[73] Males typically take flight before the females. Males then use visual cues to find a common mating ground, for example, a landmark such as a pine tree to which other males in the area converge. Males secrete a mating pheromone that females follow. Males will mount females in the air, but the actual mating process usually takes place on the ground. Females of some species mate with just one male but in others they may mate with as many as ten or more different males, storing the sperm in their spermathecae.[74]

Mated females then seek a suitable place to begin a colony. There, they break off their wings and begin to lay and care for eggs. The females can selectively fertilise future eggs with the sperm stored to produce diploid workers or lay unfertilized haploid eggs to produce drones. The first workers to hatch are known as nanitics,[75] and are weaker and smaller than later workers, but they begin to serve the colony immediately. They enlarge the nest, forage for food, and care for the other eggs. Species that have multiple queens may have a queen leaving the nest along with some workers to found a colony at a new site,[74] a process akin to swarming in honeybees.

Behaviour and ecology

Communication

Two *Camponotus sericeus* workers communicating through touch and pheromones

Ants communicate with each other using pheromones, sounds, and touch.[76] The use of pheromones as chemical signals is more developed in ants, such as the red harvester ant, than in other hymenopteran groups. Like other insects, ants perceive smells with their long, thin, and mobile antennae. The paired antennae provide information about the direction and intensity of scents. Since most ants live on the ground, they use the soil surface to leave pheromone trails that may be followed by other ants. In species that forage in groups, a forager that finds food marks a trail on the way back to the colony; this trail is followed by other ants, these ants then reinforce the trail when they head back with food to the colony. When the food source is exhausted, no new trails are marked by returning ants and the scent slowly dissipates. This behaviour helps ants deal with changes in their environment. For instance, when an established path to a food source is blocked by an obstacle, the foragers leave the path to explore new routes. If an ant is successful, it leaves a new trail marking the shortest route on its return. Successful trails are followed by more ants, reinforcing better routes and gradually identifying the best path.[77]

Ants use pheromones for more than just making trails. A crushed ant emits an alarm pheromone that sends nearby ants into an attack frenzy and attracts more ants from farther away. Several ant species even use "propaganda pheromones" to confuse enemy ants and make them fight among themselves.[78] Pheromones are produced by a wide range of structures including Dufour's glands, poison glands and glands on the hindgut, pygidium, rectum, sternum, and hind tibia.[65] Pheromones also are exchanged, mixed with food, and passed by trophallaxis, transferring information within the colony.[79] This allows other ants to detect what task group (e.g., foraging or nest maintenance) other colony members belong to.[80] In ant species with queen castes, when the dominant queen stops producing a specific pheromone, workers begin to raise new queens in the colony.[81]

Some ants produce sounds by stridulation, using the gaster segments and their mandibles. Sounds may be used to communicate with colony members or with other species.[82][83]

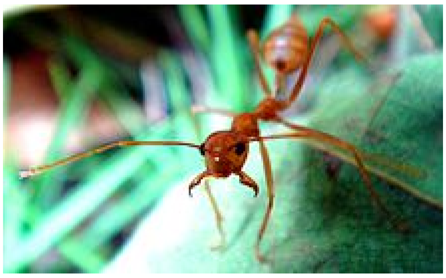
Defence

A *Plectroctena* sp. attacks another of its kind to protect its territory.

Ants attack and defend themselves by biting and, in many species, by stinging, often injecting or spraying chemicals, such as formic acid in the case of formicine ants, alkaloids and piperidines in fire ants, and a variety of protein components in other ants. Bullet ants (*Paraponera*), located in Central and South America, are considered to have the most painful sting of any insect, although it is usually not fatal to humans. This sting is given the highest rating on the Schmidt Sting Pain Index.

The sting of jack jumper ants can be fatal,[84] and an antivenom has been developed for it.[85]

Fire ants, *Solenopsis* spp., are unique in having a venom sac containing piperidine alkaloids.[86] Their stings are painful and can be dangerous to hypersensitive people.[87]



A weaver ant in fighting position, mandibles wide open

Trap-jaw ants of the genus *Odontomachus* are equipped with mandibles called trap-jaws, which snap shut faster than any other predatory appendages within the animal kingdom.[88] One study of *Odontomachus bauri* recorded peak speeds of between 126 and 230 km/h (78 and 143 mph), with the jaws closing within 130 microseconds on average. The ants were also observed to use their jaws as a catapult to eject intruders or fling themselves backward to escape a threat.[88] Before striking, the ant opens its mandibles extremely widely and locks them in this position by an internal mechanism. Energy is stored in a thick band of muscle and explosively released when triggered by the stimulation of sensory organs resembling hairs on the inside of the mandibles. The mandibles also permit slow and fine movements for other tasks. Trap-jaws also are seen in the following genera: *Anochetus*, *Orectognathus*, and *Strumigenys*,[88] plus some members of the Dacetini tribe,[89] which are viewed as examples of convergent evolution.

A Malaysian species of ant in the *Camponotus cylindricus* group has enlarged mandibular glands that extend into their gaster. If combat takes a turn for the worse, a worker may perform a final act of suicidal altruism by rupturing the membrane of its gaster, causing the content of its mandibular glands to burst from the anterior region of its head, spraying a poisonous, corrosive secretion containing acetophenones and other chemicals that immobilise small insect attackers. The worker subsequently dies.[90]

Suicidal defences by workers are also noted in a Brazilian ant, *Forelius pusillus*, where a small group of ants leaves the security of the nest after sealing the entrance from the outside each evening.[91]

Ant mound holes prevent water from entering the nest during rain.

In addition to defence against predators, ants need to protect their colonies from pathogens. Some worker ants maintain the hygiene of the colony and their activities include undertaking or *necrophory*, the disposal of dead nest-mates.[92] Oleic acid has been identified as the compound released from dead ants that triggers necrophoric behaviour in *Atta mexicana*[93] while workers of *Linepithema humile* react to the absence of characteristic chemicals (dolichodial and iridomyrmecin) present on the cuticle of their living nestmates to trigger similar behaviour.[94]

Nests may be protected from physical threats such as flooding and overheating by elaborate nest architecture.[95][96] Workers of *Cataulacus muticus*, an arboreal species that lives in plant hollows, respond to flooding by drinking water inside the nest, and excreting it outside.[97] *Camponotus anderseni*, which nests in the cavities of wood in mangrove habitats, deals with submergence under water by switching to anaerobic respiration.[98]

Learning

Many animals can learn behaviours by imitation, but ants may be the only group apart from mammals where interactive teaching has been observed. A knowledgeable forager of *Temnothorax albipennis* will lead a naive nest-mate to newly discovered food by the process of tandem running. The follower obtains knowledge through its leading tutor. The leader is acutely sensitive to the progress of the follower and slows down when the follower lags and speeds up when the follower gets too close.[99]

Controlled experiments with colonies of *Cerapachys biroi* suggest that an individual may choose nest roles based on her previous experience. An entire generation of identical workers was divided into two groups whose outcome in food foraging was controlled. One group was continually rewarded with prey, while it was made certain that the other failed. As a result, members of the successful group intensified their foraging attempts while the unsuccessful group ventured out fewer and fewer times. A month later, the successful foragers continued in their role while the others had moved to specialise in brood care.[100]

Nest construction

Leaf nest of weaver ants, Pamalican, Philippines

Complex nests are built by many ant species, but other species are nomadic and do not build permanent structures. Ants may form subterranean nests or build them on trees. These nests may be found in the ground, under stones or logs, inside logs, hollow stems, or even acorns. The materials used for construction include soil and plant matter,[74] and ants carefully select their nest sites; *Temnothorax albipennis* will avoid sites with dead ants, as these may indicate the presence of pests or disease. They are quick to abandon established nests at the first sign of threats.[101]

The army ants of South America, such as the *Eciton burchellii* species, and the driver ants of Africa do not build permanent nests, but instead, alternate between nomadism and stages where the workers form a temporary nest (bivouac) from their own bodies, by holding each other together.[102]

Weaver ant (*Oecophylla* spp.) workers build nests in trees by attaching leaves together, first pulling them together with bridges of workers and then inducing their larvae to produce silk as they are moved along the leaf edges. Similar forms of nest construction are seen in some species of *Polyrhachis*.[103]

Formica polyctena, among other ant species, constructs nests that maintain a relatively constant interior temperature that aids in the development of larvae. The ants maintain the nest temperature by choosing the location, nest materials, controlling ventilation and maintaining the heat from solar radiation, worker activity and metabolism, and in some moist nests, microbial activity in the nest materials.[104]

Some ant species, such as those that use natural cavities, can be opportunistic and make use of the controlled micro-climate provided inside human dwellings and other artificial structures to house their colonies and nest structures.[105][106]

Ant bridge

Cultivation of food

Myrmecocystus, honeypot ants, store food to prevent colony famine

Most ants are generalist predators, scavengers, and indirect herbivores,[27] but a few have evolved specialised ways of obtaining nutrition. It is believed that many ant species that engage in indirect herbivory rely on specialized symbiosis with their gut microbes [107] to upgrade the nutritional value of the food they collect [108] and allow them to survive in nitrogen poor regions, such as rainforest canopies.[109] Leafcutter ants (*Atta* and *Acromyrmex*) feed exclusively on a fungus that grows only within their colonies. They continually collect leaves which are taken to the colony, cut into tiny pieces and placed in fungal gardens. Ergates specialise in related tasks according to their sizes. The largest ants cut stalks, smaller workers chew the leaves and the smallest tend the fungus. Leafcutter ants are sensitive enough to recognise the reaction of the fungus to different plant material, apparently detecting chemical signals from the fungus. If a particular type of leaf is found to be toxic to the fungus, the colony will no longer collect it. The ants feed on structures produced by the fungi called *gongylidia*. Symbiotic bacteria on the exterior surface of the ants produce antibiotics that kill bacteria introduced into the nest that may harm the fungi.[110]

Navigation

Foraging ants travel distances of up to 200 metres (700 ft) from their nest [111] and scent trails allow them to find their way back even in the dark. In hot and arid regions, day-foraging ants face death by desiccation, so the ability to find the shortest route back to the nest reduces that risk. Diurnal desert ants of the genus *Cataglyphis* such as the Sahara desert ant navigate by keeping track of direction as well as distance travelled. Distances travelled are measured using an internal pedometer that keeps count of the steps taken[112] and also by evaluating the movement of objects in their visual field (optical flow).[113] Directions are measured using the position of the sun.[114] They integrate this information to find the shortest route back to their nest.[115] Like all ants, they can also make use of visual landmarks when available[116] as well as olfactory and tactile cues to navigate.[117][118] Some species of ant are able to use the Earth's magnetic field for navigation.[119] The compound eyes of ants have specialised cells that detect polarised light from the Sun, which is used to determine direction.[120][121] These polarization detectors are sensitive in the ultraviolet region of the light spectrum.[122] In some army ant species, a group of foragers who become separated from the main column may sometimes turn back on themselves and form a circular ant mill. The workers may then run around continuously until they die of exhaustion.[123]

An ant trail

Locomotion

Play media

Ant in Slow Motion

The female worker ants do not have wings and reproductive females lose their wings after their mating flights in order to begin their colonies. Therefore, unlike their wasp ancestors, most ants travel by walking. Some species are capable of leaping. For example, Jerdon's jumping ant (*Harpegnathos saltator*) is able to jump by synchronising the action of its mid and hind pairs of legs.[124] There are several species of gliding ant including *Cephalotes atratus*; this may be a common trait among arboreal ants with small colonies. Ants with this ability are able to control their horizontal movement so as to catch tree trunks when they fall from atop the forest canopy.[125]

Other species of ants can form chains to bridge gaps over water, underground, or through spaces in vegetation. Some species also form floating rafts that help them survive floods.[126] These rafts may also have a role in allowing ants to colonise islands.[127] *Polyrhachis sokolova*, a species of ant found in Australian mangrove swamps, can swim and live in underwater nests. Since they lack gills, they go to trapped pockets of air in the submerged nests to breathe.[128]

Cooperation and competition

Not all ants have the same kind of societies. The Australian bulldog ants are among the biggest and most basal of ants. Like virtually all ants, they are eusocial, but their social behaviour is poorly developed compared to other species. Each individual hunts alone, using her large eyes instead of chemical senses to find prey.[129]

Meat-eater ants feeding on a cicada: social ants cooperate and collectively gather food

Some species (such as *Tetramorium caespitum*) attack and take over neighbouring ant colonies. Others are less expansionist, but just as aggressive; they invade colonies to steal eggs or larvae, which they either eat or raise as workers or slaves. Extreme specialists among these slave-raiding ants, such as the Amazon ants, are incapable of feeding themselves and need captured workers to survive.[130] Captured workers of enslaved *Temnothorax* species have evolved a counter strategy, destroying just the female pupae of the slave-making *Temnothorax americanus*, but sparing the males (who don't take part in slave-raiding as adults).[131]

A worker *Harpegnathos saltator* (a jumping ant) engaged in battle with a rival colony's queen

Ants identify kin and nestmates through their scent, which comes from hydrocarbon-laced secretions that coat their exoskeletons. If an ant is separated from its original colony, it will eventually lose the colony scent. Any ant that enters a colony without a matching scent will be attacked.[132] Also, the reason why two separate colonies of ants will attack each other even if they are of the same species is because the genes responsible for pheromone production are different between them. The Argentine ant, however, does not have this characteristic, due to lack of genetic diversity, and has become a global pest because of it.

Parasitic ant species enter the colonies of host ants and establish themselves as social parasites; species such as *Strumigenys xenos* are entirely parasitic and do not have workers, but instead, rely on the food gathered by their *Strumigenys perplexa* hosts.[133][134] This form of parasitism is seen across many ant genera, but the parasitic ant is usually a species that is closely related to its host. A variety of methods are employed to enter the nest of the host ant. A parasitic queen may enter the host nest before the first brood has hatched, establishing herself prior to development of a colony scent. Other species use pheromones to confuse the host ants or to trick them into carrying the parasitic queen into the nest. Some simply fight their way into the nest.[135]

A conflict between the sexes of a species is seen in some species of ants with these reproducers apparently competing to produce offspring that are as closely related to them as possible. The most extreme form involves the production of clonal offspring. An extreme of sexual conflict is seen in *Wasmannia auropunctata*, where the queens produce diploid daughters by thelytokous parthenogenesis and males produce clones by a process whereby a diploid egg loses its maternal contribution to produce haploid males who are clones of the father.[136]

Relationships with other organisms

Ants form symbiotic associations with a range of species, including other ant species, other insects, plants, and fungi. They also are preyed on by many animals and even certain fungi. Some arthropod species spend part of their lives within ant nests, either preying on ants, their larvae, and eggs, consuming the food stores of the ants, or avoiding predators. These inquilines may bear a close resemblance to ants. The nature of this ant mimicry (myrmecomorphy) varies, with some cases involving Batesian mimicry, where the mimic reduces the risk of predation. Others show Wasmannian mimicry, a form of mimicry seen only in inquilines.[137][138]

The spider *Myrmarachne plataleoides* (female shown) mimics weaver ants to avoid predators.

An ant collects honeydew from an aphid

Aphids and other hemipteran insects secrete a sweet liquid called honeydew, when they feed on plant sap. The sugars in honeydew are a high-energy food source, which many ant species collect.[139] In some cases, the aphids secrete the honeydew in response to ants tapping them with their antennae. The ants in turn keep predators away from the aphids and will move them from one feeding location to another. When migrating to a new area, many colonies will take the aphids with them, to ensure a continued supply of honeydew. Ants also tend mealybugs to harvest their honeydew. Mealybugs may become a serious pest of pineapples if ants are present to protect mealybugs from their natural enemies.[140]

Myrmecophilous (ant-loving) caterpillars of the butterfly family Lycaenidae (e.g., blues, coppers, or hairstreaks) are herded by the ants, led to feeding areas in the daytime, and brought inside the ants' nest at night. The caterpillars have a gland which secretes honeydew when the ants massage them. Some caterpillars produce vibrations and sounds that are perceived by the ants.[141] A similar adaptation can be seen in Grizzled skipper butterflies that emit vibrations by expanding their wings in order to communicate with ants, which are natural predators of these butterflies.[142] Other caterpillars have evolved from ant-loving to ant-eating: these myrmecophagous caterpillars secrete a pheromone that makes the ants act as if the caterpillar is one of their own larvae. The caterpillar is then taken into the ant nest where it feeds on the ant larvae.[143] A number of specialized bacterial have been found as endosymbionts in ant guts. Some of the dominant bacteria belong to the order Rhizobiales whose members are known for being nitrogen-fixing symbionts in legumes but the species found in ant lack the ability to fix nitrogen.[144][145] Fungus-growing ants that make up the tribe Attini, including leafcutter ants, cultivate certain species of fungus in the genera *Leucoagaricus* or *Leucocoprinus* of the family Agaricaceae. In this ant-fungus mutualism, both species depend on each other for survival. The ant *Allomerus decemarticulatus* has evolved a three-way association with the host plant, *Hirtella physophora* (Chrysobalanaceae), and a sticky fungus which is used to trap their insect prey.[146]

Lemon ants make devil's gardens by killing surrounding plants with their stings and leaving a pure patch of lemon ant trees, (*Duroia hirsuta*). This modification of the forest provides the ants with more nesting sites inside the stems of the *Duroia* trees.[147] Although some ants obtain nectar from flowers, pollination by ants is somewhat rare, one example being of the pollination of the orchid *Leporella fimbriata* which induces male *Myrmecia urens* to pseudocopulate with the flowers, transferring pollen in the process.[148] One theory that has been proposed for the rarity of pollination is that the secretions of the metapleural gland inactivate and reduce the viability of pollen.[149][150] Some plants have special nectar exuding structures, extrafloral nectaries, that provide food for ants, which in turn protect the plant from more damaging herbivorous insects.[151] Species such as the bullhorn acacia (*Acacia cornigera*) in Central America have

Ants may obtain nectar from flowers such as the dandelion but are only rarely known to pollinate flowers.

hollow thorns that house colonies of stinging ants (*Pseudomyrmex ferruginea*) who defend the tree against insects, browsing mammals, and epiphytic vines. Isotopic labelling studies suggest that plants also obtain nitrogen from the ants.[152] In return, the ants obtain food from protein- and lipid-rich Beltian bodies. In Fiji *Philidris nagasau* (Dolichoderinae) are known to selectively grow species of epiphytic *Squamellaria* (Rubiaceae) which produce large domatia inside which the ant colonies nest. The ants plant the seeds and the domatia of young seedling are immediately occupied and the ant faeces in them contribute to rapid growth.[153] Similar dispersal associations are found with other dolichoderines in the region as well.[154] Another example of this type of ectosymbiosis comes from the *Macaranga* tree, which has stems adapted to house colonies of *Crematogaster* ants.[155]

Many plant species have seeds that are adapted for dispersal by ants.[156] Seed dispersal by ants or myrmecochory is widespread, and new estimates suggest that nearly 9% of all plant species may have such ant associations.[157][156] Often, seed-dispersing ants perform directed dispersal, depositing the seeds in locations that increase the likelihood of seed survival to reproduction.[158] Some plants in arid, fire-prone systems are particularly dependent on ants for their survival and dispersal as the seeds are transported to safety below the ground.[159] Many ant-dispersed seeds have special external structures, elaiosomes, that are sought after by ants as food.[160]

A convergence, possibly a form of mimicry, is seen in the eggs of stick insects. They have an edible elaiosome-like structure and are taken into the ant nest where the young hatch.[161]

A meat ant tending a common leafhopper nymph

Most ants are predatory and some prey on and obtain food from other social insects including other ants. Some species specialise in preying on termites (*Megaponera* and *Termitopone*) while a few Cerapachyinae prey on other ants.[111] Some termites, including *Nasutitermes corniger*, form associations with certain ant species to keep away predatory ant species.[162] The tropical wasp *Mischocyttarus drewseni* coats the pedicel of its nest with an ant-repellent chemical.[163] It is suggested that many tropical wasps may build their nests in trees and cover them to protect themselves from ants. Other wasps, such as *A. multipicta*, defend against ants by blasting them off the nest with bursts of wing buzzing.[164] Stingless bees (*Trigona* and *Melipona*) use chemical defences against ants.[111]

Flies in the Old World genus *Bengalia* (Calliphoridae) prey on ants and are kleptoparasites, snatching prey or brood from the mandibles of adult ants.[165] Wingless and legless females of the Malaysian phorid fly (*Vestigipoda myrmolarvoidea*) live in the nests of ants of the genus *Aenictus* and are cared for by the ants.[165]

Fungi in the genera *Cordyceps* and *Ophiocordyceps* infect ants. Ants react to their infection by climbing up plants and sinking their mandibles into plant tissue. The fungus kills the ants, grows on their remains, and produces a fruiting body. It appears that the fungus alters the behaviour of the ant to help disperse its spores [166] in a microhabitat that best suits the fungus.[167] Strepsipteran parasites also manipulate their ant host to climb grass stems, to help the parasite find mates.[168]

A nematode (*Myrmeconema neotropicum*) that infects canopy ants (*Cephalotes atratus*) causes the black-coloured gasters of workers to turn red. The parasite also alters the behaviour of the ant, causing them to carry their gasters high. The conspicuous red gasters are mistaken by birds for ripe fruits, such as *Hyeronima alchorneoides*, and eaten. The droppings of the bird are collected by other ants and fed to their young, leading to further spread of the nematode.[169]

South American poison dart frogs in the genus *Dendrobates* feed mainly on ants, and the toxins in their skin may come from the ants.[170]

Army ants forage in a wide roving column, attacking any animals in that path that are unable to escape. In Central and South America, *Eciton burchellii* is the swarming ant most commonly attended by "ant-following" birds such as antbirds and woodcreepers.[171][172] This behaviour was once considered mutualistic, but later studies found the birds to be parasitic. Direct

kleptoparasitism (birds stealing food from the ants' grasp) is rare and has been noted in Inca doves which pick seeds at nest entrances as they are being transported by species of *Pogonomyrmex*.[173] Birds that follow ants eat many prey insects and thus decrease the foraging success of ants.[174] Birds indulge in a peculiar behaviour called anting that, as yet, is not fully understood. Here birds rest on ant nests, or pick and drop ants onto their wings and feathers; this may be a means to remove ectoparasites from the birds.

Spiders sometimes feed on ants.

Anteaters, aardvarks, pangolins, echidnas and numbats have special adaptations for living on a diet of ants. These adaptations include long, sticky tongues to capture ants and strong claws to break into ant nests. Brown bears (*Ursus arctos*) have been found to feed on ants. About 12%, 16%, and 4% of their faecal volume in spring, summer, and autumn, respectively, is composed of ants.[175]

Relationship with humans

Weaver ants are used as a biological control for citrus cultivation in southern China.

Ants perform many ecological roles that are beneficial to humans, including the suppression of pest populations and aeration of the soil. The use of weaver ants in citrus cultivation in southern China is considered one of the oldest known applications of biological control.[14] On the other hand, ants may become nuisances when they invade buildings, or cause economic losses.

In some parts of the world (mainly Africa and South America), large ants, especially army ants, are used as surgical sutures. The wound is pressed together and ants are applied along it. The ant seizes the edges of the wound in its mandibles and locks in place. The body is then cut off and the head and mandibles remain in place to close the wound.[176][177][178] The large heads of the dinergates (soldiers) of the leafcutting ant *Atta cephalotes* are also used by native surgeons in closing wounds.[179]

Some ants have toxic venom and are of medical importance. The species include *Paraponera clavata* (tocandira) and *Dinoponera* spp. (false tocandiras) of South America [180] and the *Myrmecia* ants of Australia.[181]

In South Africa, ants are used to help harvest the seeds of rooibos (*Aspalathus linearis*), a plant used to make a herbal tea. The plant disperses its seeds widely, making manual collection difficult. Black ants collect and store these and other seeds in their nest, where humans can gather them *en masse*. Up to half a pound (200 g) of seeds may be collected from one ant-heap.[182][183]

Although most ants survive attempts by humans to eradicate them, a few are highly endangered. These tend to be island species that have evolved specialized traits and risk being displaced by introduced ant species. Examples include the critically endangered Sri Lankan relict ant (*Aneuretus simoni*) and *Adetomyrma venatrix* of Madagascar.[184]

It has been estimated by E.O. Wilson that the total number of individual ants alive in the world at any one time is between one and ten quadrillion (short scale) (i.e., between 10^{15} and 10^{16}). According to this estimate, the total biomass of all the ants in the world is approximately equal to the total biomass of the entire human race.[185] Also, according to this estimate, there are approximately 1 million ants for every human on Earth.[186]

As food

Roasted ants in Colombia

Ant larvae for sale in Isaan, Thailand

Ants and their larvae are eaten in different parts of the world. The eggs of two species of ants are used in Mexican *escamoles*. They are considered a form of insect caviar and can sell for as much as US$40 per pound ($90/kg) because they are seasonal and hard to find. In the Colombian department of Santander, *hormigas culonas* (roughly interpreted as "large-bottomed ants") *Atta laevigata* are toasted alive and eaten.[187]

In areas of India, and throughout Burma and Thailand, a paste of the green weaver ant (*Oecophylla smaragdina*) is served as a condiment with curry.[188] Weaver ant eggs and larvae, as well as the ants, may be used in a Thai salad, *yam* (Thai: ยำ), in a dish called *yam khai mot daeng* (Thai: ยำไข่มดแดง) or red ant egg salad, a dish that comes from the Issan or north-eastern region of Thailand. Saville-Kent, in the *Naturalist in Australia* wrote "Beauty, in the case of the green ant, is more than skin-deep. Their attractive, almost sweetmeat-like translucency possibly invited the first essays at their consumption by the human species". Mashed up in water, after the manner of lemon squash, "these ants form a pleasant acid drink which is held in high favor by the natives of North Queensland, and is even appreciated by many European palates".[189]

In his *First Summer in the Sierra*, John Muir notes that the Digger Indians of California ate the tickling, acid gasters of the large jet-black carpenter ants. The Mexican Indians eat the replete workers, or living honey-pots, of the honey ant (*Myrmecocystus*).[189]

As pests

Some ant species are considered as pests, primarily those that occur in human habitations, where their presence is often problematic. For example, the presence of ants would be undesirable in sterile places such as hospitals or kitchens. Some species or genera commonly categorized as pests include the Argentine ant, pavement ant, yellow crazy ant, banded sugar ant, pharaoh ant, carpenter ants, odorous house ant, red imported fire ant, and European fire ant. Some ants will raid stored food, others may damage indoor structures, some can damage agricultural crops directly (or by aiding sucking pests), and some will sting or bite.[15] The adaptive nature of ant colonies make it nearly impossible to eliminate entire colonies and most pest management practices aim to control local populations and tend to be temporary solutions. Ant populations are managed by a combination of approaches that make use of chemical, biological and physical methods. Chemical methods include the use of insecticidal bait which is gathered by ants as food and brought back to the nest where the poison is inadvertently spread to other colony members through trophallaxis. Management is based on the species and techniques can vary according to the location and circumstance.[15]

The tiny pharaoh ant is a major pest in hospitals and office blocks; it can make nests between sheets of paper.

In science and technology

Observed by humans since the dawn of history, the behaviour of ants has been documented and the subject of early writings and fables passed from one century to another. Those using scientific methods, myrmecologists, study ants in the laboratory and in their natural conditions. Their complex and variable social structures have made ants ideal model organisms. Ultraviolet vision

was first discovered in ants by Sir John Lubbock in 1881.[190] Studies on ants have tested hypotheses in ecology and sociobiology, and have been particularly important in examining the predictions of theories of kin selection and evolutionarily stable strategies.[191] Ant colonies may be studied by rearing or temporarily maintaining them in *formicaria*, specially constructed glass framed enclosures.[192] Individuals may be tracked for study by marking them with dots of colours.[193]

Camponotus nearcticus workers travelling between two formicaria through connector tubing

The successful techniques used by ant colonies have been studied in computer science and robotics to produce distributed and fault-tolerant systems for solving problems, for example Ant colony optimization and Ant robotics. This area of biomimetics has led to studies of ant locomotion, search engines that make use of "foraging trails", fault-tolerant storage, and networking algorithms.[13]

As pets

From the late 1950s through the late 1970s, ant farms were popular educational children's toys in the United States. Some later commercial versions use transparent gel instead of soil, allowing greater visibility at the cost of stressing the ants with unnatural light.[194]

In culture

Aesop's ants: picture by Milo Winter, 1888–1956

Anthropomorphised ants have often been used in fables and children's stories to represent industriousness and cooperative effort. They also are mentioned in religious texts.[195][196] In the Book of Proverbs in the Bible, ants are held up as a good example for humans for their hard work and cooperation.[197] Aesop did the same in his fable The Ant and the Grasshopper. In the Quran, Sulayman is said to have heard and understood an ant warning other ants to return home to avoid being accidentally crushed by Sulayman and his marching army. [Quran 27:18 (http://www.perseus.tufts.edu/hopper/text?doc=Perseus%3Atext%3A2002.02.0006%3Asura%3D27%3Averse%3D18)][198] In parts of Africa, ants are considered to be the messengers of the deities. Some Native American mythology, such as the Hopi mythology, considers ants as the very first animals. Ant bites are often said to have curative properties. The sting of some species of *Pseudomyrmex* is claimed to give fever relief.[199] Ant bites are used in the initiation ceremonies of some Amazon Indian cultures as a test of endurance.[200][201]

Ant society has always fascinated humans and has been written about both humorously and seriously. Mark Twain wrote about ants in his 1880 book *A Tramp Abroad*.[202] Some modern authors have used the example of the ants to comment on the relationship between society and the individual. Examples are Robert Frost in his poem "Departmental" and T. H. White in his fantasy novel *The Once and Future King*. The plot in French entomologist and writer Bernard Werber's *Les Fourmis* science-fiction trilogy is divided between the worlds of ants and humans; ants and their behaviour is described using contemporary scientific knowledge. H.G. Wells wrote about intelligent ants destroying human settlements in Brazil and threatening human civilization in his 1905 science-fiction short story, *The Empire of the Ants.* In more recent times, animated cartoons and 3-D animated films featuring ants have been produced including *Antz*, *A Bug's Life*, *The Ant Bully*, *The Ant and the Aardvark*, *Ferdy the Ant* and *Atom Ant.* Renowned myrmecologist E. O. Wilson wrote a short story, "Trailhead" in 2010 for *The New Yorker*

magazine, which describes the life and death of an ant-queen and the rise and fall of her colony, from an ants' point of view.[203] The French neuroanatomist, psychiatrist and eugenicist Auguste Forel believed that ant societies were models for human society. He published a five volume work from 1921 to 1923 that examined ant biology and society.[204]

In the early 1990s, the video game *SimAnt*, which simulated an ant colony, won the 1992 Codie award for "Best Simulation Program".[205]

Ants also are quite popular inspiration for many science-fiction insectoids, such as the Formics of *Ender's Game*, the Bugs of *Starship Troopers*, the giant ants in the films *Them!* and *Empire of the Ants*, Marvel Comics' super hero Ant-Man, and ants mutated into super-intelligence in *Phase IV*. In computer strategy games, ant-based species often benefit from increased production rates due to their single-minded focus, such as the Klackons in the *Master of Orion* series of games or the ChCht in *Deadlock II*. These characters are often credited with a hive mind, a common misconception about ant colonies.[206]

See also

- Ant robotics
- Ant venom
- Glossary of ant terms
- International Union for the Study of Social Insects
- *Myrmecological News* (journal)
- Task allocation and partitioning of social insects

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House dust mite

House dust mites (**HDM**, or simply **dust mites**) are mites found in association with dust in dwellings.[1]

House dust mites (*Dermatophagoides pteronyssinus*) aggregate

The main species are:

- *Dermatophagoides farinae* (American house dust mite)
- *Dermatophagoides microceras*
- *Dermatophagoides pteronyssinus* (European house dust mite)
- *Euroglyphus maynei* (Mayne's house dust mite)

Contents

Biology

Taxonomy

The dust mites are cosmopolitan members of the mite family Pyroglyphidae.

Characteristics

House dust mites, due to their very small size and translucent bodies, are barely visible to the unaided eye.[2] A typical house dust mite measures 0.2–0.3 mm (0.008–0.012 in) in length.[3] For accurate identification, one needs at least 10× magnification. The body of the house dust mite has a striated cuticle.

Diet


A scanning electron micrograph of a female dust mite

They feed on skin flakes from animals, including humans, and on some mold. *Dermatophagoides farinae* fungal food choices in 16 tested species commonly found in homes was observed *in vitro* to be *Alternaria alternata*, *Cladosporium sphaerospermum*, and *Wallemia sebi*, and they disliked *Penicillium chrysogenum*, *Aspergillus versicolor*, and *Stachybotrys chartarum*.[4]

Predators

The predators of dust mites are other allergenic mites (*Cheyletiella*), silverfish and pseudoscorpions.[5]

Reproduction

The average life cycle for a house dust mite is 65–100 days.[6] A mated female house dust mite can live up to 70 days, laying 60 to 100 eggs in the last five weeks of her life. In a 10-week life span, a house dust mite will produce approximately 2,000 fecal particles and an even larger number of partially digested enzyme-covered dust particles.

Distribution

Dust mites are found worldwide, but are found more commonly in humid regions.[7] The species *Blomia tropicalis* is typically found only in tropical or subtropical regions.[8] Detectable dust mite allergen was found in the beds of about 84% of surveyed United States homes.[9] In Europe, detectable Der p 1 or Der f 1 allergen was found in 68% of surveyed homes.[10]

Health issues

Allergies

The mite's gut contains potent digestive enzymes (notably Peptidase 1) that persist in their feces and are major inducers of allergic reactions such as wheezing. The mite's exoskeleton can also contribute to allergic reactions. Unlike scabies mites or skin follicle mites, house dust mites do not burrow under the skin and are not parasitic.[11]

Severe dust mite infestation in the home has been linked to atopic dermatitis and epidermal barrier damage has been documented.[12]

House dust mites are associated with allergic rhinitis and asthma,[13] as well as allergic conjunctivitis.[14] Efforts to remove these mites from the environment have not been found to be effective.[13] Immunotherapy may be useful in those affected.[13] Subcutaneous injections have better evidence than under the tongue dosing.[15] Topical steroids as nasal spray or inhalation may be used.[16]

Oral mite anaphylaxis

Dermatophagoides spp. can cause oral mite anaphylaxis (AKA pancake syndrome) when found in flour.[17][18]

Control techniques

House dust mites are present indoors wherever humans live. Positive tests for dust mite allergies are extremely common among people with asthma. Dust mites are microscopic arachnids whose primary food is dead human skin cells, but they do not live on living people. They and their feces and other allergens which they produce are major constituents of house dust, but because they are so heavy they are not suspended for long in the air. They are generally found on the floor and other surfaces until disturbed (by walking, for example). It could take somewhere between twenty minutes and two hours for dust mites to settle back down out of the air.

Dust mites are a nesting species that prefers a dark, warm, and humid climate. They flourish in mattresses, bedding, upholstered furniture, and carpets. Their feces include enzymes that are released upon contact with a moist surface, which can happen when a person inhales, and these enzymes can kill cells within the human body.[19] House dust mites did not become a problem until humans began to use textiles, such as western style blankets and clothing.[20]

Furniture

Furniture with wooden or leather surfaces reduce the dust mite population.[21]

Bed linen

Hot tumble drying a bed linen for 1 hour will kill 99% of mites therein.[22]

Weekly changing the bed linen reduces the risk of exposure to dust mites.[16]

Cotton covers not covered with complete mattress covers are very likely to become colonised by bacteria and molds; they must be cleaned periodically (at least every second to third month).[23]

Dust mite eggs are freeze tolerant (−70 °C for 30 minutes); hatching can normally be prevented by exposure of fabrics to:[24]

- Direct sunlight for 3 hours or
- Dry or wet heat of at least 60 °C (140 °F) for a minimum of 30 minutes.

Dust mite-proof encasements to mattress, pillow, and duvet, prevents chronic contact with allergens.[16][21]

Dust mites drown in water.[25]

Good properties of anti-mite fabrics have been identified as being:[26]

- Thread count greater than 246.
- Pore size of between 2 and 10 microns.
- Allergen impenetrability >99%.
- Dust leakage of less than 4%.
- Breathability between 2 and 6 cm^3/second/cm^2.

Indoor climate

Allergy patients are advised to keep the relative humidity below 50%, if possible. Very few mites can survive if the humidity is less than 45% (at 22 °C (72 °F)). However, they can survive if the humidity is high just for an hour and a half per day, for example due to cooking.[25]

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Earwig

Earwigs make up the insect order **Dermaptera**. With about 2,000 species[1] in 12 families, they are one of the smaller insect orders. Earwigs have characteristic cerci, a pair of forceps-like pincers on their abdomen, and membranous wings folded underneath short, rarely used forewings, hence the scientific order name, "skin wings". Some groups are tiny parasites on mammals and lack the typical pincers. Earwigs are found on all continents except Antarctica.

Earwigs are mostly nocturnal and often hide in small, moist crevices during the day, and are active at night, feeding on a wide variety of insects and plants. Damage to foliage, flowers, and various crops is commonly blamed on earwigs, especially the common earwig *Forficula auricularia.*

Earwigs have five molts in the year before they become adults. Many earwig species display maternal care, which is uncommon among insects. Female earwigs may care for their eggs, and even after they have hatched as nymphs will continue to watch over offspring until their second molt. As the nymphs molt, sexual dimorphism such as differences in pincer shapes begins to show.

Some earwig specimen fossils are in the extinct suborders Archidermaptera or Eodermaptera, the former dating to the Late Triassic and the latter to the Middle Jurassic. Many orders of insect have been theorized to be closely related to earwigs, though the icebugs of Notoptera are most likely.

Earwig

Temporal range: 208–0 Ma

PreЄ Є O S D C P T J K PgN

Late Triassic to Recent

Female common earwig, *Forficula auricularia*

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Infraclass:	Neoptera
Superorder:	Exopterygota
Order:	Dermaptera De Geer, 1773

Suborders

- †Archidermaptera
- †Eodermaptera
- Neodermaptera

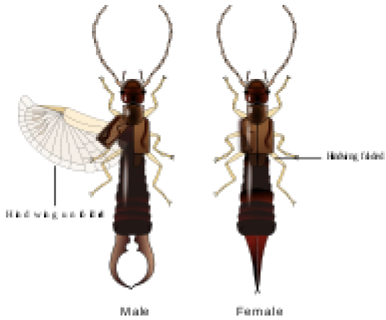
Synonyms

- Euplecoptera
- Euplexoptera
- Forficulida

Contents

Etymology

The scientific name for the order, "Dermaptera", is Greek in origin, stemming from the words *derma*, meaning skin, and *pteron* (plural *ptera*), wing. It was coined by Charles De Geer in 1773. The common term, *earwig*, is derived from the Old English *ēare*, which means "ear", and *wicga*, which means "insect", or literally, "beetle".[2] Entomologists suggest that the origin of the name is a reference to the appearance of the hindwings, which are unique and distinctive among insects, and resemble a human ear when unfolded.[3][4] The name is more popularly thought to be related to the old wives' tale that earwigs burrowed into the brains of humans through the ear and laid their eggs there.[5] Earwigs are not known to purposefully climb into ear canals, but there have been anecdotal reports of earwigs being found in the ear.[6]



Earwig diagram with wings extended and closed

Distribution

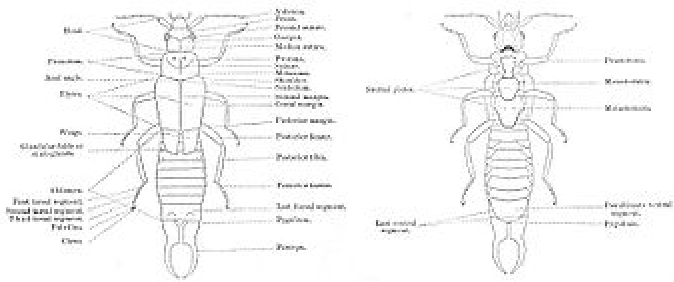
Earwigs are abundant and can be found throughout the Americas and Eurasia. The common earwig was introduced into North America in 1907 from Europe, but tends to be more common in the southern and southwestern parts of the United States.[7]:739 The only native species of earwig found in the north of the United States is the spine-tailed earwig (*Doru aculeatum*),[8]:144 found as far north as Canada, where it hides in the leaf axils of emerging plants in southern Ontario wetlands. However, other families can be found in North America, including Forficulidae (*Doru* and *Forficula* being found there), Spongiphoridae, Anisolabididae, and Labiduridae.[9]


An earwig from the Western Ghats

Few earwigs survive winter outdoors in cold climates. They can be found in tight crevices in woodland, fields and gardens.[7]:739[10] Out of about 1,800 species, about 25 occur in North America, 45 in Europe (including 7 in Great Britain), and 60 in Australia.[11]

Morphology

Most earwigs are flattened (which allows them to fit inside tight crevices, such as under bark) with an elongated body generally 7–50 millimetres (0.28–1.97 in) long.[11] The largest extant species is the Australian giant earwig (*Titanolabis colossea*) which is approximately 50 mm (2.0 in) long,[12]:10 while the possibly extinct Saint Helena earwig (*Labidura herculeana*) reached 78 mm (3.1 in).[13] Earwigs are characterized by the cerci, or the pair of forceps-like pincers on their abdomen; male earwigs generally have more curved pincers than females. These pincers are used to capture prey, defend themselves and fold their wings under the short tegmina.[14] The antennae are thread-like with at least 10 segments.[7]:738–739


Male earwig, external morphology. Click on image for a larger view

The forewings are short oblong leathery plates used to cover the hindwings like the elytra of a beetle, rather than to fly. Most species have short and leather-like forewings with very thin hindwings, though species in the former suborders Arixeniina and Hemimerina (epizoic species, sometimes considered as ectoparasites[15][16]) are wingless and blind with filiform segmented cerci (today these are both included merely as families in the suborder Neodermaptera).[11][17][18] The hindwing is a very thin membrane that expands like a fan, radiating from one point folded under the forewing. Even though most earwigs have wings and are capable of flight, they are rarely seen in flight. These wings are unique in venation and in the pattern of folding that requires the use of the cerci.[19]

Internal

The neuroendocrine system is typical of insects. There is a brain, a subesophageal ganglion, three thoracic ganglia, and six abdominal ganglia. Strong neuron connections connect the neurohemal corpora cardiaca to the brain and frontal ganglion, where the closely related median corpus allatum produces juvenile hormone III in close proximity to the neurohemal dorsal arota. The digestive system of earwigs is like all other insects, consisting of a fore-, mid-, and hindgut, but earwigs lack gastric caecae which are specialized for digestion in many species of insect. Long, slender (excretory) malpighian tubules can be found between the junction of the mid- and hind gut.[20]

The reproductive system of females consist of paired ovaries, lateral oviducts, spermatheca, and a genital chamber. The lateral ducts are where the eggs leave the body, while the spermatheca is where sperm is stored. Unlike other insects, the gonopore, or genital opening is behind the seventh abdominal segment. The ovaries are primitive in that they are polytrophic (the nurse cells and oocytes alternate along the length of the ovariole). In some species these long ovarioles branch off the lateral duct, while in others, short ovarioles appear around the duct.[20]

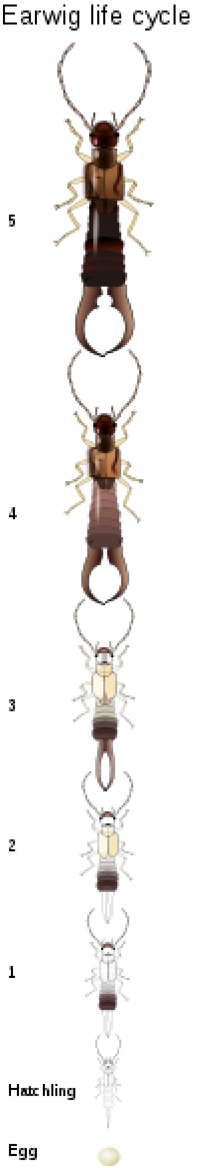
Life cycle and reproduction

Earwigs are hemimetabolous, meaning they undergo incomplete metamorphosis, developing through a series of 4 to 6 molts. The developmental stages between molts are called instars. Earwigs live for about a year from hatching. They start mating in the autumn, and can be found together in the autumn and winter. The male and female will live in a chamber in debris, crevices, or soil 2.5 centimetres (1 in) deep.[7]:739 After mating, the sperm may remain in the female for months before the eggs are fertilized. From midwinter to early spring, the male will leave, or be driven out by the female. Afterward the female will begin to lay 20 to 80 pearly white eggs in 2 days. Some earwigs, those parasitic in the suborders Arixeniina and Hemimerina, are viviparous (give birth to live young); they would be fed by a sort of placenta.[7]:739–740[17] When first laid, the eggs are white or cream-colored and oval-shaped, but right before hatching they become kidney-shaped and brown.[21] Each egg is approximately 1 mm (0.04 in) tall and 0.8 mm (0.03 in) wide.[18]

Earwigs are among the few non-social insect species that show maternal care. The mother will pay close attention to the needs of her eggs, such as warmth and protection, though studies have shown that the mother does not pay attention to the eggs as she collects them.[17] The mother has been shown to pick up wax balls by accident, but they would eventually be rejected as they do not have the proper scent. The mother will also faithfully defend the eggs from predators, not leaving them to eat unless the clutch goes bad.[7]:740 Another distinct maternal care unique to earwigs is that the mother continuously cleans the eggs to protect them from fungi. Studies have found that the urge to clean the eggs persists for days after they are removed; when the eggs were replaced after hatching, the mother continued to clean them for up to 3 months.[17]

Female earwig in her nest, with eggs

Female earwig in her nest with newly hatched young



The life cycle and development of a male earwig from egg to each instar

The eggs hatch in about 7 days. The mother may assist the nymphs in hatching. When the nymphs hatch, they eat the egg casing and continue to live with the mother. The nymphs look similar to their parents, only smaller, and will nest under their mother and she will continue to protect them until their second molt. The nymphs feed on food regurgitated by the mother,[22] and on their own molts. If the mother dies before the nymphs are ready to leave, the nymphs may eat her.[7]:740[23]

An earwig on a wall in Haldia, West Bengal, India.

An earwig on a wooden door in Haldia, West Bengal, India.

After five to six instars, the nymphs will molt into adults. The male's forceps will become curved, while the females' forceps remain straight. They will also develop their natural color, which can be anything from a light brown (as in the Tawny earwig) to a dark black (as in the Ringlegged earwig). In species of winged earwigs, the wings will start to develop at this time. The forewings of an earwig are sclerotized to serve as protection for the membranous hindwings.

Behavior

Most earwigs are nocturnal and inhabit small crevices, living in small amounts of debris, in various forms such as bark and fallen logs. Species have been found to be blind and living in caves, or cavernicolous, reported to be found on the island of Hawaii and in South Africa. Food typically consists of a wide array of living and dead plant and animal matter.[20] For protection from predators, the species *Doru taeniatum* of earwigs can squirt foul-smelling yellow liquid in the form of jets from scent glands on the dorsal side of the third and fourth abdominal segment. It aims the discharges by revolving the abdomen, a maneuver that enables it simultaneously to use its pincers in defense.[24]

Ecology

Earwigs are mostly scavengers, but some are omnivorous or predatory.[7]:739–740 The abdomen of the earwig is flexible and muscular. It is capable of maneuvering as well as opening and closing the forceps. The forceps are used for a variety of purposes. In some species, the forceps have been observed in use for holding prey, and in copulation. The forceps tend to be more curved in males than in females.[25]

A male of *Forficula auricularia* feeding on flowers.

The common earwig is an omnivore, eating plants and ripe fruit as well as actively hunting arthropods. To a large extent, this species is also a scavenger, feeding on decaying plant and animal matter if given the chance. Observed prey include largely plant lice, but also large insects such as bluebottle flies and woolly aphids.[10] Plants that they feed on typically include clover, dahlias, zinnias, butterfly bush, hollyhock, lettuce, cauliflower, strawberry, blackberry, sunflowers, celery, peaches, plums, grapes, potatoes, roses, seedling beans and beets, and tender grass shoots and roots; they have also been known to eat corn silk, damaging the corn.[26]

Species of the suborders Arixeniina and Hemimerina are generally considered epizoic, or living on the outside of other animals, mainly mammals. In the Arixeniina, family Arixeniidae, species of the genus *Arixenia* are normally found deep in the skin folds and gular pouch of Malaysian hairless bulldog bats (*Cheiromeles torquatus*), apparently feeding on bats' body or glandular secretions. On the other hand, species in the genus *Xeniaria* (still of the suborder Arixeniina) are believed to feed on the guano and possibly the guanophilous arthropods in the bat's roost, where it has been found. Hemimerina includes *Araeomerus* found in the nest of Long-tailed pouch rats (*Beamys*), and *Hemimerus* which are found on Giant *Cricetomys* rats.[16][27]

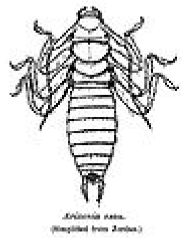
Earwigs are generally nocturnal, and typically hide in small, dark, and often moist areas in the daytime. They can usually be seen on household walls and ceilings. Interaction with earwigs at this time results in a defensive free-fall to the ground followed by a scramble to a nearby cleft or crevice.[25] During the summer they can be found around damp areas such as near sinks and in bathrooms. Earwigs tend to gather in shady cracks or openings or anywhere that they can remain concealed during daylight. Picnic tables, compost and waste bins, patios, lawn furniture, window frames, or anything with minute spaces (even artichoke blossoms) can potentially harbour them.[28]

Predators and parasites

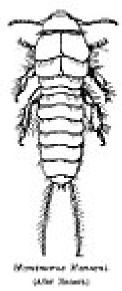
Earwigs are regularly preyed upon by birds, and like many other insect species they are prey for insectivorous mammals, amphibians, lizards, centipedes, assassin bugs, and spiders.[29] European naturalists have observed bats preying upon earwigs.[29] Their primary insect predators are parasitic species of Tachinidae, or tachinid flies, whose larvae are endoparasites. One species of tachinid fly, *Triarthria setipennis*, has been demonstrated to be successful as a biological control of earwigs for almost a century.[30][31] Another tachinid fly and parasite of earwigs, *Ocytata pallipes*, has shown promise as a biological control agent as well.[32] The common predatory wasp, the yellow jacket (*Vespula maculifrons*), preys upon earwigs when abundant.[33] A small species of roundworm, *Mermis nigrescens*, is known to occasionally parasitize earwigs that have consumed roundworm eggs with plant matter.[34] At least 26 species of parasitic fungus from the order Laboulbeniales have been found on earwigs.[35] The eggs and nymphs are also cannibalized by other earwigs.[36] A species of tyroglyphoid mite, *Histiostoma polypori* (Histiostomatidae, Astigmata), are observed on common earwigs, sometimes in great densities;[37] however, this mite feeds on earwig cadavers and not its live earwig transportation.[38] Hippolyte Lucas observed scarlet acarine mites on European earwigs.[39]

Evolution

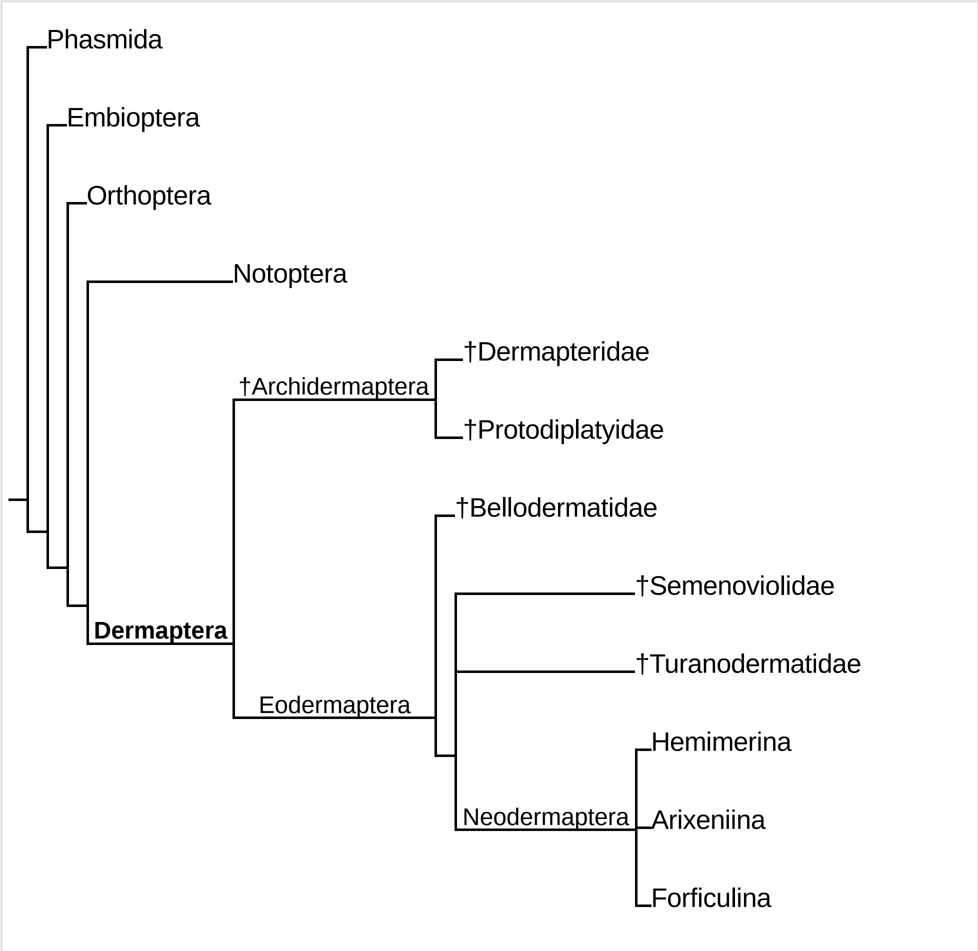
The fossil record of the Dermaptera starts in the Late Triassic to Early Jurassic period about 208 million years ago in England and Australia, and comprises about 70 specimens in the extinct suborder Archidermaptera. Some of the traits believed by neontologists to belong to modern earwigs are not found in the earliest fossils, but adults had five-segmented tarsi (the final segment of the leg), well developed ovipositors, veined tegmina (forewings) and long segmented cerci; in fact the pincers would not have been curled or used as they are now.[14] The theorized stem group of the Dermaptera are the Protelytroptera. These insects, which resemble modern Blattodea, or cockroaches owing to shell-like forewings and the large, unequal anal fan, are known from the Permian of North America, Europe and Australia. There are no fossils from the Triassic when the morphological changes from Protelytroptera to Dermaptera took place.[42] The most likely, and most closely resembling, related order of insects is Notoptera, theorized by Giles in 1963. However, other arguments have been made by other authors linking them to Phasmida, Embioptera, Plecoptera, and Dictyoptera.[11]



Arixenia esau from the extinct suborder Arixeniina



Hemimerus hanseni from the extinct suborder Hemimerina



Earwigs and their relatives[40][41]

Archidermaptera is believed to be sister to the remaining earwig groups, the extinct Eodermaptera and the living suborder Neodermaptera (= former suborders Forficulina, Hemimerina, and Arixeniina). The extinct suborders have tarsi with five segments (unlike the three found in Neodermaptera) as well as unsegmented cerci. No fossil Hemimeridae and Arixeniidae are known.[43] Species in Hemimeridae were at one time in their own order, Diploglassata, Dermodermaptera, or Hemimerina. Like most other epizoic species, there is no fossil record, but they are probably no older than late Tertiary.[14]

Some evidence of early evolutionary history is the structure of the antennal heart, a separate circulatory organ consisting of two ampullae, or vesicles,[44] that are attached to the frontal cuticle to the bases of the antennae.[45] These features have not been found in other insects. An independent organ exists for each antenna, consisting of an ampulla, attached to the frontal cuticle medial to the antenna base and forming a thin-walled sac with a valved ostium on its ventral side. They pump blood by elastic connective tissue, rather than muscle.[46]

Molecular studies suggest that this order is the sister to Plecoptera or to Ephemeroptera.[47]

Taxonomy

Distinguishing characteristics

The characteristics which distinguish the order Dermaptera from other insect orders are:[48]

- *General body shape*: Elongate; dorso-ventrally flattened.
- *Head*: Prognathous. Antennae are segmented. Biting-type mouthparts. Ocelli absent. Compound eyes in most species, reduced or absent in some taxa.
- *Appendages*: Two pairs of wings normally present. The forewings are modified into short smooth, veinless tegmina. Hindwings are membranous and semicircular with veins radiating outwards.
- *Abdomen*: Cerci are unsegmented and resemble forceps. The ovipositor in females is reduced or absent.

The overwhelming majority of earwig species are in Forficulina, grouped into nine families of 180 genera,[42] including *Forficula auricularia*, the common European Earwig. Species within Forficulina are free-living, have functional wings and are not parasites. The cerci are unsegmented and modified into large, forceps-like structures.

The first epizoic species of earwig was discovered by a London taxidermist on the body of a Malaysian hairless bulldog bat in 1909, then described by Karl Jordan. By the 1950s, the two suborders *Arixeniina* and *Hemimerina* had been added to Dermaptera.[16]

Arixeniina represents two genera, *Arixenia* and *Xeniaria,* with a total of five species in them. As with Hemimerina, they are blind and wingless, with filiform segmented cerci. Hemimerina are viviparous ectoparasites, preferring the fur of African rodents in either *Cricetomys* or *Beamys* genera.[43] Hemimerina also has two genera, *Hemimerus* and *Araeomerus*, with a total of 11 species.[43]

Phylogeny

Dermaptera is relatively small compared to the other orders of Insecta, with only about 2,000 species, 3 suborders and 15 families, including the extinct suborders Archidermaptera and Eodermaptera with their extinct families Protodiplatyidae, Dermapteridae, Semenoviolidae, and Turanodermatidae. The phylogeny of the Dermaptera is still debated. The extant Dermaptera appear to be monophyletic and there is support for the monophyly of the families Forficulidae, Chelisochidae, Labiduridae and Anisolabididae, however evidence has supported the conclusion that the former suborder Forficulina was paraphyletic through the exclusion of Hemimerina and Arixeniina which should instead be nested within the Forficulina.[42][49] Thus, these former suborders were eliminated in the most recent higher classification.

A female of the common earwig in a threat pose

Relationship with humans

Earwigs are fairly abundant and are found in many areas around the world. There is no evidence that they transmit diseases to humans or other animals. Their pincers are commonly believed to be dangerous, but in reality, even the curved pincers of males cause little or no harm to humans.[50] Earwigs have been rarely known[51] to crawl into the ears of humans, but they do not lay eggs inside the human body or human brain.[52][53]

There is a debate whether earwigs are harmful or beneficial to crops, as they eat both the foliage and the insects eating such foliage, such as aphids, though it would take a large population to do considerable damage. The common earwig eats a wide variety of plants, and also a wide variety of foliage, including the leaves and petals. They have been known to cause economic losses in fruit and vegetable crops. Some examples are the flowers, hops, red raspberries,[54] and corn crops in Germany, and in the south of France, earwigs have been observed feeding on peaches and apricots. The earwigs attacked mature plants and made cup-shaped bite marks 3–11 mm (0.12–0.43 in) in diameter.[55]

In literature and folklore

- Oscar Cook wrote the short story (appearing in *Switch On The Light*, April, 1931; *A Century Of Creepy Stories* 1934; *Pan Horror 2*, 1960) *Boomerang*, which was later adapted by Rod Serling for the Night Gallery tv-series episode, *The Caterpillar*.[56] It tells the tale of the use of an earwig as a murder instrument applied by a man obsessed with the wife of an associate.
- Robert Herrick in *Hesperides* describes a feast attended by Queen Titania through writing: "Beards of mice, a newt's stew'd thigh, A bloated Earwig and a fly".
- Thomas Hood discusses the myth of earwigs finding shelter in the human ear in the poem "Love Lane" by saying the following: "'Tis vain to talk of hopes and fears, / And hope the least reply to wing, / From any maid that stops her ears / In dread of earwigs creeping in!"[57]
- In some parts of rural England the earwig is called "battle-twig", which is present in Alfred, Lord Tennyson's poem *The Spinster's Sweet-Arts*: "'Twur as bad as battle-twig 'ere i' my oan blue chamber to me."[58]
- In some regions of Japan, earwigs are called "Chinpo-Basami" or "Chinpo-Kiri", which means "penis cutter". Kenta Takada, a Japanese cultural entomologist, has inferred that these names may be derived from the fact that earwigs were seen around old Japanese-style toilets.[59]
- In George's Marvellous Medicine, George's Grandma encourages him to eat unwashed celery with beetles and earwigs still on them. "A big fat earwig is very tasty,' Grandma said, licking her lips. 'But you've got to be very quick, my dear, when you put one of those in your mouth. It has a pair of sharp nippers on its back end and if it grabs your tongue with those, it never lets go. So you've got to bite the earwig first, chop chop, before it bites you."[60]

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WIKIPEDIA

Fly

Fly
Temporal range: 245 –0 Ma
PreЄ Є O S D C P T J K PgN
Middle Triassic – Recent

Syrphus ribesii, showing characteristic dipteran features: large eyes, small antennae, sucking mouthparts, single pair of flying wings, hindwings reduced to clublike halteres

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Superorder:	Panorpida
(unranked):	Antliophora
Order:	Diptera Linnaeus, 1758

True **flies** are insects of the order **Diptera**, the name being derived from the Greek δι- *di*- "two", and πτερόν *pteron* "wings". Insects of this order use only a single pair of wings to fly, the hindwings having evolved into advanced mechanosensory organs known as halteres, which act as high-speed sensors of rotational movement and allow dipterans to perform advanced aerobatics.[1] Diptera is a large order containing an estimated 1,000,000 species including horse-flies,[a] crane flies, hoverflies and others, although only about 125,000 species have been described.[4]

Flies have a mobile head, with a pair of large compound eyes, and mouthparts designed for piercing and sucking (mosquitoes, black flies and robber flies), or for lapping and sucking in the other groups. Their wing arrangement gives them great maneuverability in flight, and claws and pads on their feet enable them to cling to smooth surfaces. Flies undergo complete metamorphosis; the eggs are laid on the larval food-source and the larvae, which lack true limbs, develop in a protected environment, often inside their food source. The pupa is a tough capsule from which the adult emerges when ready to do so; flies mostly have short lives as adults.

Diptera is one of the major insect orders and of considerable ecological and human importance. Flies are important pollinators, second only to the bees and their Hymenopteran relatives. Flies may have been among the evolutionarily earliest pollinators responsible for early plant pollination. Fruit flies are used as model organisms in research, but less benignly, mosquitoes are vectors for malaria, dengue, West Nile fever, yellow fever, encephalitis, and other infectious diseases; and houseflies, commensal with humans all over the world, spread food-borne illnesses. Flies can be annoyances especially in some parts of the world where they can occur in large numbers, buzzing and settling on the skin or eyes to bite or seek fluids. Larger flies such as tsetse flies and screwworms cause significant economic harm to cattle. Blowfly larvae, known as gentles, and other dipteran larvae, known more generally as maggots, are used as fishing bait and as food for carnivorous animals. They are also used in medicine in debridement to clean wounds.

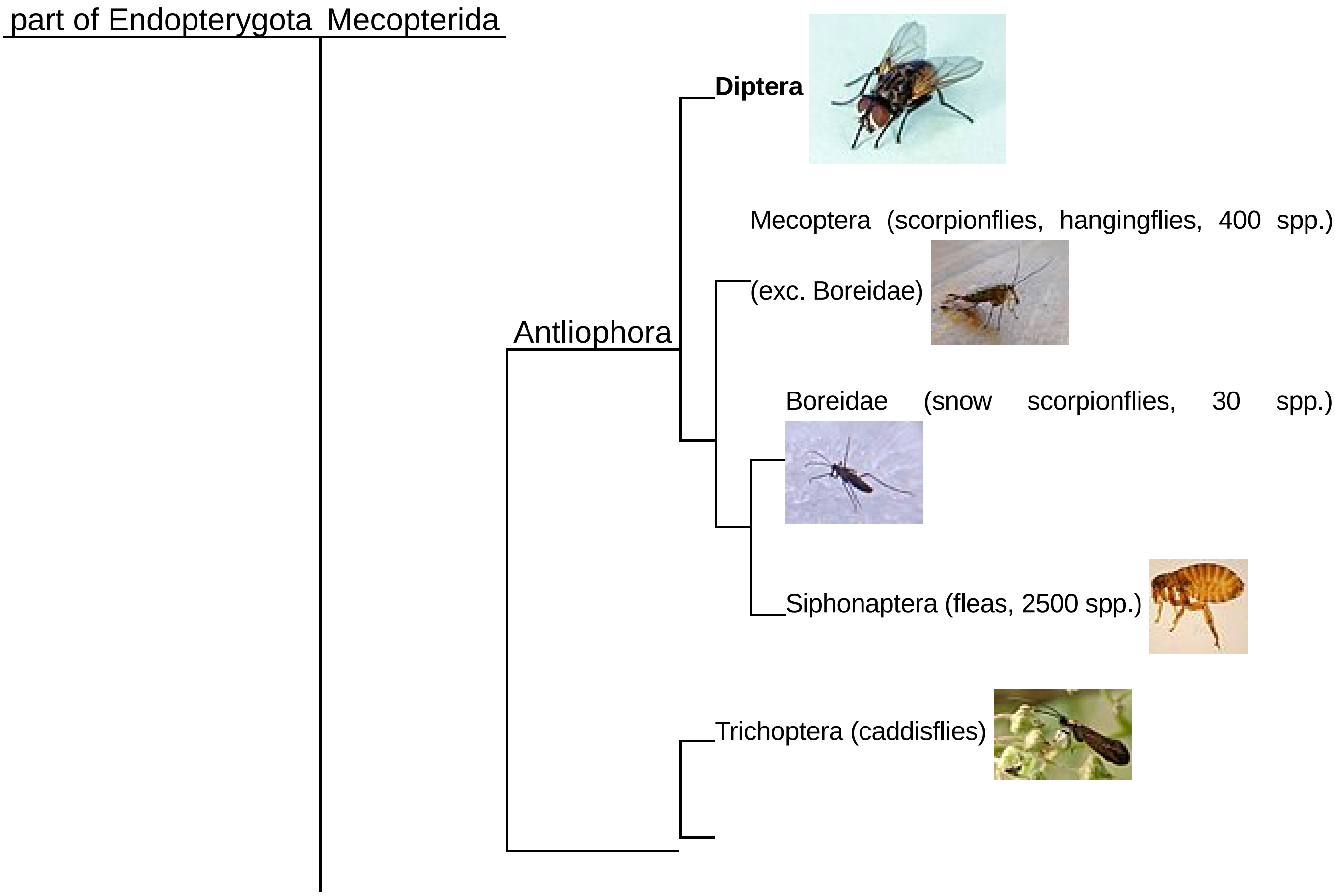
Contents

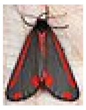
Taxonomy and phylogeny

Relationships to other insects

Dipterans are endopterygotes, insects that undergo radical metamorphosis. They belong to the Mecopterida, alongside the Mecoptera, Siphonaptera, Lepidoptera and Trichoptera.[5][6] The possession of a single pair of wings distinguishes most true flies from other insects with "fly" in their names. However, some true flies such as Hippoboscidae (louse flies) have become secondarily wingless.[7]

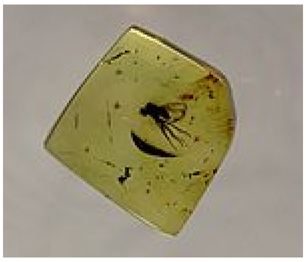
The cladogram represents the current consensus view.[8]



Lepidoptera (butterflies and moths) 

Hymenoptera (sawflies, wasps, ants, bees) 

Relationships between fly subgroups and families



Fossil brachyceran in Baltic amber. Lower Eocene, c. 50 million years ago

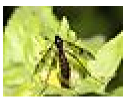
Fossil nematoceran in Dominican amber. Sandfly, *Lutzomyia adiketis* (Psychodidae), Early Miocene, c. 20 million years ago

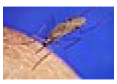
The first true dipterans known are from the Middle Triassic (around 240 million years ago), and they became widespread during the Middle and Late Triassic.[9] Modern flowering plants did not appear until the Cretaceous (around 140 million years ago), so the original dipterans must have had a different source of nutrition other than nectar. Based on the attraction of many modern fly groups to shiny droplets, it has been suggested that they may have fed on honeydew produced by sap-sucking bugs which were abundant at the time, and dipteran mouthparts are well-adapted to softening and lapping up the crusted residues.[10] The basal clades in the Diptera include the Deuterophlebiidae and the enigmatic Nymphomyiidae.[11] Three episodes of evolutionary radiation are thought to have occurred based on the fossil record. Many new species of lower Diptera developed in the Triassic, about 220 million years ago. Many lower Brachycera appeared in the Jurassic, some 180 million years ago. A third radiation took place among the Schizophora at the start of the Paleogene, 66 million years ago.[11]

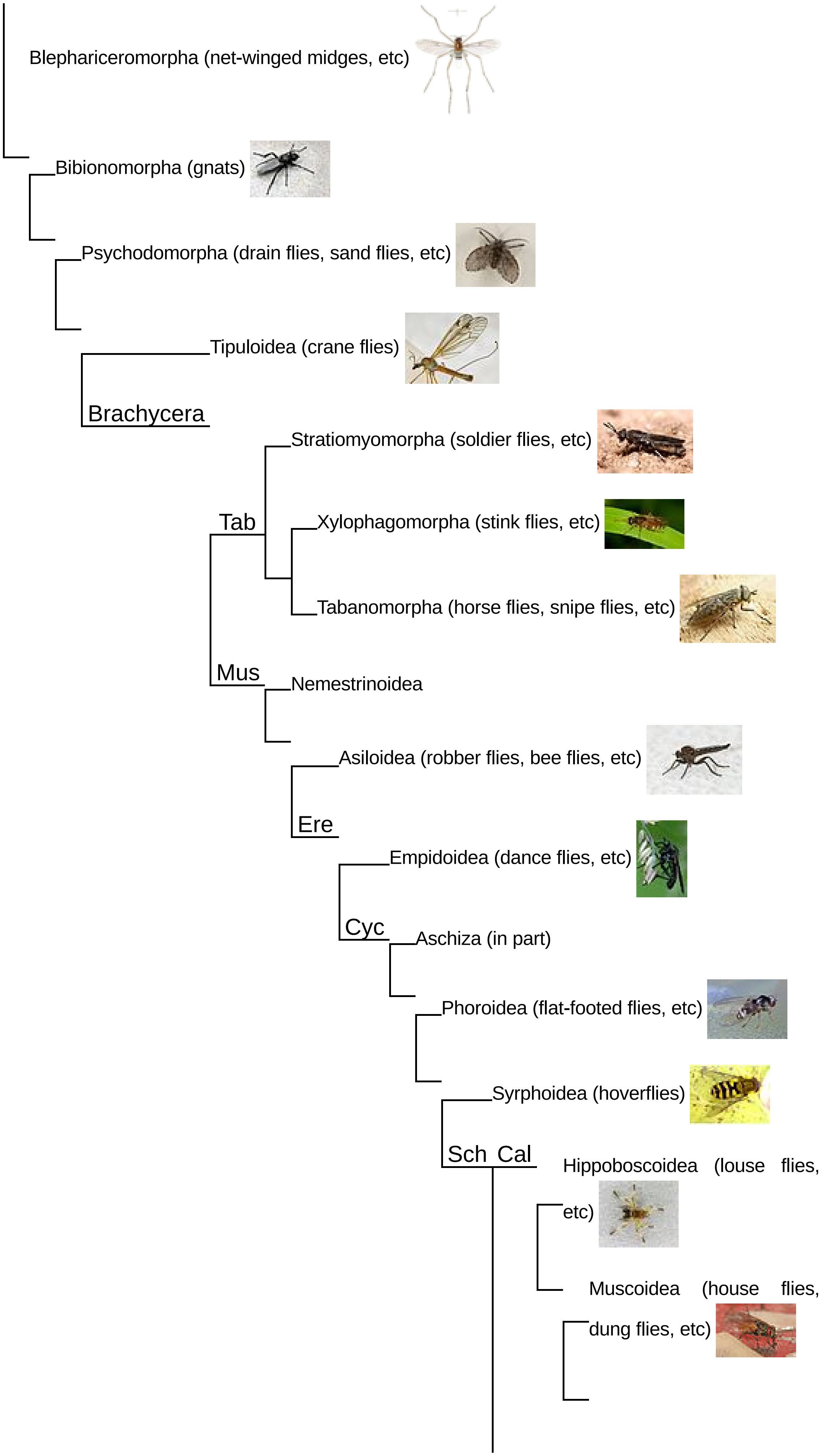
The phylogenetic position of Diptera has been controversial. The monophyly of holometabolous insects has long been accepted, with the main orders being established as Lepidoptera, Coleoptera, Hymenoptera and Diptera, and it is the relationships between these groups which has caused difficulties. Diptera is widely thought to be a member of Mecopterida, along with Lepidoptera (butterflies and moths), Trichoptera (caddisflies), Siphonaptera (fleas), Mecoptera (scorpionflies) and possibly Strepsiptera (twisted-wing flies). Diptera has been grouped with Siphonaptera and Mecoptera in the Antliophora, but this has not been confirmed by molecular studies.[12]

Diptera were traditionally broken down into two suborders, Nematocera and Brachycera, distinguished by the differences in antennae. The Nematocera are identified by their elongated bodies and many-segmented, often feathery antennae as represented by mosquitoes and crane flies. The Brachycera have rounder bodies and much shorter antennae.[13][14] Subsequent studies have identified the Nematocera as being non-monophyletic with modern phylogenies placing the Brachycera within grades of groups formerly placed in the Nematocera. The construction of a phylogenetic tree has been the subject of ongoing research. The following cladogram is based on the FLYTREE project.[11][15][16]

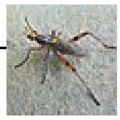
Nematocera

Ptychopteromorpha (phantom and primitive crane-flies) 

Culicomorpha (mosquitoes) 


Blephariceromorpha (net-winged midges, etc)
Bibionomorpha (gnats)
Psychodomorpha (drain flies, sand flies, etc)
Tipuloidea (crane flies)
Brachycera
Stratiomyomorpha (soldier flies, etc)
Tab
Xylophagomorpha (stink flies, etc)
Tabanomorpha (horse flies, snipe flies, etc)
Mus
Nemestrinoidea
Asiloidea (robber flies, bee flies, etc)
Ere
Empidoidea (dance flies, etc)
Cyc
Aschiza (in part)
Phoroidea (flat-footed flies, etc)
Syrphoidea (hoverflies)
Sch Cal
Hippoboscoidea (louse flies, etc)
Muscoidea (house flies, dung flies, etc)

Oestroidea (blow flies, flesh flies, etc) 

Acalyptratae (marsh flies, etc) 

Abbreviations used in the cladogram:

- Cal=Calyptratae
- Cyc=Cyclorrhapha
- Ere=Eremoneura
- Mus=Muscomorpha
- Sch=Schizophora
- Tab=Tabanomorpha

Diversity

Gauromydas heros is the largest fly in the world.

Flies are often abundant and are found in almost all terrestrial habitats in the world apart from Antarctica. They include many familiar insects such as house flies, blow flies, mosquitoes, gnats, black flies, midges and fruit flies. More than 150,000 have been formally described and the actual species diversity is much greater, with the flies from many parts of the world yet to be studied intensively.[17][18] The suborder Nematocera include generally small, slender insects with long antennae such as mosquitoes, gnats, midges and crane-flies, while the Brachycera includes broader, more robust flies with short antennae. Many nematoceran larvae are aquatic.[19] There are estimated to be a total of about 19,000 species of Diptera in Europe, 22,000 in the Nearctic region, 20,000 in the Afrotropical region, 23,000 in the Oriental region and 19,000 in the Australasian region.[20] While most species have restricted distributions, a few like the housefly (*Musca domestica*) are cosmopolitan.[21] *Gauromydas heros* (Asiloidea), with a length of up to 7 cm (2.8 in), is generally considered to be the largest fly in the world,[22] while the smallest is *Euryplatea nanaknihali*, which at 0.4 mm (0.016 in) is smaller than a grain of salt.[23]

Brachycera are ecologically very diverse, with many being predatory at the larval stage and some being parasitic. Animals parasitised include molluscs, woodlice, millipedes, insects, mammals,[20] and amphibians.[24] Flies are the second largest group of pollinators after the Hymenoptera (bees, wasps and relatives). In wet and colder environments flies are significantly more important as pollinators. Compared to bees, they need less food as they do not need to provision their young. Many flowers that bear low nectar and those that have evolved trap pollination depend on flies.[25] It is thought that some of the earliest pollinators of plants may have been flies.[26]

The greatest diversity of gall forming insects are found among the flies, principally in the family Cecidomyiidae (gall midges).[27] Many flies (most importantly in the family Agromyzidae) lay their eggs in the mesophyll tissue of leaves with larvae feeding between the surfaces forming blisters and mines.[28] Some families are mycophagous or fungus feeding. These include the cave dwelling Mycetophilidae (fungus gnats) whose larvae are the only diptera with bioluminescence. The Sciaridae are also fungus feeders. Some plants are pollinated by fungus feeding flies that visit fungus infected male flowers.[29]

The larvae of *Megaselia scalaris* (Phoridae) are almost omnivorous and consume such substances as paint and shoe polish.[30] The *Exorista mella (Walker)* fly are considered generalists and parasitoids of a variety of hosts[31]. The larvae of the shore flies (Ephydridae) and some Chironomidae survive in extreme environments including glaciers (*Diamesa* sp., Chironomidae[32]), hot springs, geysers, saline pools, sulphur pools, septic tanks and even crude oil (*Helaeomyia petrolei*[32]).[20] Adult hoverflies (Syrphidae) are well known for their mimicry and the larvae adopt diverse lifestyles including being inquiline scavengers inside the nests of social insects.[33] Some brachycerans are agricultural pests, some bite animals and humans and suck their blood, and some transmit diseases.[20]

Anatomy and morphology

Flies are adapted for aerial movement and typically have short and streamlined bodies. The first tagma of the fly, the head, bears the eyes, the antennae, and the mouthparts (the labrum, labium, mandible, and maxilla make up the mouthparts). The second tagma, the thorax, bears the wings and contains the flight muscles on the second segment, which is greatly enlarged; the first and third segments have been reduced to collar-like structures, and the third segment bears the halteres, which help to balance the insect during flight. The third tagma is the abdomen consisting of 11 segments, some of which may be fused, and with the 3 hindmost segments modified for reproduction.[34] Some Dipterans are mimics and can only be distinguished from their models by very careful inspection. An example of this is *Spilomyia longicornis*, which is a fly but mimics a vespid wasp.

Head of *a horse-fly* showing large compound eyes and stout piercing mouthparts

Flies have a mobile head with a pair of large compound eyes on the sides of the head, and in most species, three small ocelli on the top. The compound eyes may be close together or widely separated, and in some instances are divided into a dorsal region and a ventral region, perhaps to assist in swarming behaviour. The antennae are well-developed but variable, being thread-like, feathery or comb-like in the different families. The mouthparts are adapted for piercing and sucking, as in the black flies, mosquitoes and robber flies, and for lapping and sucking as in many other groups.[34] Female horse-flies use knife-like mandibles and maxillae to make a cross-shaped incision in the host's skin and then lap up the blood that flows. The gut includes large diverticulae, allowing the insect to store small quantities of liquid after a meal.[35]

For visual course control, flies' optic flow field is analyzed by a set of motion-sensitive neurons.[36] A subset of these neurons is thought to be involved in using the optic flow to estimate the parameters of self-motion, such as yaw, roll, and sideward translation.[37] Other neurons are thought to be involved in analyzing the content of the visual scene itself, such as separating figures from the ground using motion parallax.[38][39] The H1 neuron is responsible for detecting horizontal motion across the entire visual field of the fly, allowing the fly to generate and guide stabilizing motor corrections midflight with respect to yaw.[40] The ocelli are concerned in the detection of changes in light intensity, enabling the fly to react swiftly to the approach of an object.[41]

Like other insects, flies have chemoreceptors that detect smell and taste, and mechanoreceptors that respond to touch. The third segments of the antennae and the maxillary palps bear the main olfactory receptors, while the gustatory receptors are in the labium, pharynx, feet, wing margins and female genitalia,[42] enabling flies to taste their food by walking on it. The taste receptors in females at the tip of the abdomen receive information on the suitability of a site for ovipositing.[41] Flies that feed on blood have special sensory structures that can detect infrared emissions, and use them to home in on their hosts, and many blood-sucking flies can detect the raised concentration of carbon dioxide that occurs near large animals.[43] Some tachinid flies (Ormiinae) which are parasitoids of bush crickets, have sound receptors to help them locate their singing hosts.[44]

Diptera have one pair of fore wings on the mesothorax and a pair of halteres, or reduced hind wings, on the metathorax. A further adaptation for flight is the reduction in number of the neural ganglia, and concentration of nerve tissue in the thorax, a feature that is most extreme in the highly derived Muscomorpha infraorder.[35] Some species of flies are exceptional in that they are

secondarily flightless. The only other order of insects bearing a single pair of true, functional wings, in addition to any form of halteres, are the Strepsiptera. In contrast to the flies, the Strepsiptera bear their halteres on the mesothorax and their flight wings on the metathorax.[45] Each of the fly's six legs has a typical insect structure of coxa, trochanter, femur, tibia and tarsus, with the tarsus in most instances being subdivided into five tarsomeres.[34] At the tip of the limb is a pair of claws, and between these are cushion-like structures known as pulvilli which provide adhesion.[46]


A cranefly, showing the hind wings reduced to drumstick-shaped halteres

The abdomen shows considerable variability among members of the order. It consists of eleven segments in primitive groups and ten segments in more derived groups, the tenth and eleventh segments having fused.[47] The last two or three segments are adapted for reproduction. Each segment is made up of a dorsal and a ventral sclerite, connected by an elastic membrane. In some females, the sclerites are rolled into a flexible, telescopic ovipositor.[34]

Flight

Flies are capable of great manoeuvrability during flight due to the presence of the halteres. These act as gyroscopic organs and are rapidly oscillated in time with the wings; they act as a balance and guidance system by providing rapid feedback to the wing-steering muscles, and flies deprived of their halteres are unable to fly. The wings and halteres move in synchrony but the amplitude of each wing beat is independent, allowing the fly to turn sideways.[48] The wings of the fly are attached to two kinds of muscles, those used to power it and another set used for fine control.[49]


Tabanid fly in flight

Flies tend to fly in a straight line then make a rapid change in direction before continuing on a different straight path. The directional changes are called saccades and typically involve an angle of 90°, being achieved in 50 milliseconds. They are initiated by visual stimuli as the fly observes an object, nerves then activate steering muscles in the thorax that cause a small change in wing stroke which generate sufficient torque to turn. Detecting this within four or five wingbeats, the halteres trigger a counter-turn and the fly heads off in a new direction.[50]

Flies have rapid reflexes that aid their escape from predators but their sustained flight speeds are low. Dolichopodid flies in the genus *Condylostylus* respond in less than 5 milliseconds to camera flashes by taking flight.[51] In the past, the deer bot fly, *Cephenemyia*, was claimed to be one of the fastest insects on the basis of an estimate made visually by Charles Townsend in 1927.[52] This claim, of speeds of 600 to 800 miles per hour, was regularly repeated until it was shown to be physically impossible as well as incorrect by Irving Langmuir. Langmuir suggested an estimated speed of 25 miles per hour.[53][54][55]

Although most flies live and fly close to the ground, a few are known to fly at heights and a few like *Oscinella* (Chloropidae) are known to be dispersed by winds at altitudes of up to 2000 ft and over long distances.[56] Some hover flies like *Metasyrphus corollae* have been known to undertake long flights in response to aphid population spurts.[57]

Males of fly species such as *Cuterebra*, many hover flies,[58] bee flies (Bombyliidae)[59] and fruit flies (Tephritidae)[60] maintain territories within which they engage in aerial pursuit to drive away intruding males and other species.[61] While these territories may be held by individual males, some species, such as *A. freeborni*,[62] form leks with many males aggregating in displays.[60] Some flies maintain an airspace and still others form dense swarms that maintain a stationary location with respect to landmarks. Many flies mate in flight while swarming.[63]

Life cycle and development

Diptera go through a complete metamorphosis with four distinct life stages – egg, larva, pupa and adult.

Mating anthomyiid flies

Larva

In many flies, the larval stage is long and adults may have a short life. Most dipteran larvae develop in protected environments; many are aquatic and others are found in moist places such as carrion, fruit, vegetable matter, fungi and, in the case of parasitic species, inside their hosts. They tend to have thin cuticles and become desiccated if exposed to the air. Apart from the Brachycera, most dipteran larvae have sclerotinised head capsules, which may be reduced to remnant mouth hooks; the Brachycera, however, have soft, gelatinized head capsules from which the sclerites are reduced or missing. Many of these larvae retract their heads into their thorax.[34][64]

Life cycle of stable fly *Stomoxys calcitrans*, showing eggs, 3 larval instars, pupa, and adult

Some other anatomical distinction exists between the larvae of the Nematocera and the Brachycera. Especially in the Brachycera, little demarcation is seen between the thorax and abdomen, though the demarcation may be visible in many Nematocera, such as mosquitoes; in the Brachycera, the head of the larva is not clearly distinguishable from the rest of the body, and few, if any, sclerites are present. Informally, such brachyceran larvae are called maggots,[65] but the term is not technical and often applied indifferently to fly larvae or insect larvae in general. The eyes and antennae of brachyceran larvae are reduced or absent, and the abdomen also lacks appendages such as cerci. This lack of features is an adaptation to food such as carrion, decaying detritus, or host tissues surrounding endoparasites.[35] Nematoceran larvae generally have well-developed eyes and antennae, while those of Brachyceran larvae are reduced or modified.[66]

Dipteran larvae have no jointed, "true legs",[64] but some dipteran larvae, such as species of Simuliidae, Tabanidae and Vermileonidae, have prolegs adapted to hold onto a substrate in flowing water, host tissues or prey.[67] The majority of dipterans are oviparous and lay batches of eggs, but some species are ovoviviparous, where the larvae starting development inside the eggs before they hatch or viviparous, the larvae hatching and maturing in the body of the mother before being externally deposited. These are found especially in groups that have larvae dependent on food sources that are short-lived or are accessible for brief periods.[68] This is widespread in some families such as the Sarcophagidae. In *Hylemya strigosa* (Anthomyiidae) the larva moults to the second instar before hatching, and in *Termitoxenia* (Phoridae) females have incubation pouches, and a full developed third instar larva is deposited by the adult and it almost immediately pupates with no freely feeding larval stage. The tsetse fly (as well as other Glossinidae, Hippoboscidae, Nycteribidae and Streblidae) exhibits adenotrophic viviparity; a single fertilised egg is retained in the oviduct and the developing larva feeds on glandular secretions. When fully grown, the female finds a spot with soft soil and the larva works its way out of the oviduct, buries itself and pupates. Some flies like *Lundstroemia parthenogenetica* (Chironomidae) reproduce by thelytokous parthenogenesis, and some gall midges have larvae that can produce eggs (paedogenesis).[69][70]

Pupa

The pupae take various forms. In some groups, particularly the Nematocera, the pupa is intermediate between the larval and adult form; these pupae are described as "obtect", having the future appendages visible as structures that adhere to the pupal body. The outer surface of the pupa may be leathery and bear spines, respiratory features or locomotory paddles. In other groups, described as "coarctate", the appendages are not visible. In these, the outer surface is a puparium, formed from the last larval skin, and the actual pupa is concealed within. When the adult insect is ready to emerge from this tough, desiccation-resistant capsule, it inflates a balloon-like structure on its head, and forces its way out.[34]

Adult

The adult stage is usually short, its function only to mate and lay eggs. The genitalia of male flies are rotated to a varying degree from the position found in other insects.[71] In some flies, this is a temporary rotation during mating, but in others, it is a permanent torsion of the organs that occurs during the pupal stage. This torsion may lead to the anus being below the genitals, or, in the case of 360° torsion, to the sperm duct being wrapped around the gut and the external organs being in their usual position. When flies mate, the male initially flies on top of the female, facing in the same direction, but then turns around to face in the opposite direction. This forces the male to lie on his back for his genitalia to remain engaged with those of the female, or the torsion of the male genitals allows the male to mate while remaining upright. This leads to flies having more reproduction abilities than most insects, and much quicker. Flies occur in large populations due to their ability to mate effectively and quickly during the mating season.[35]

Ecology

As ubiquitous insects, dipterans play an important role at various trophic levels both as consumers and as prey. In some groups the larvae complete their development without feeding, and in others the adults do not feed. The larvae can be herbivores, scavengers, decomposers, predators or parasites, with the consumption of decaying organic matter being one of the most prevalent feeding behaviours. The fruit or detritus is consumed along with the associated micro-organisms, a sieve-like filter in the pharynx being used to concentrate the particles, while flesh-eating larvae have mouth-hooks to help shred their food. The larvae of some groups feed on or in the living tissues of plants and fungi, and some of these are serious pests of agricultural crops. Some aquatic larvae consume the films of algae that form underwater on rocks and plants. Many of the parasitoid larvae grow inside and eventually kill other arthropods, while parasitic larvae may attack vertebrate hosts.[34]

Whereas many dipteran larvae are aquatic or live in enclosed terrestrial locations, the majority of adults live above ground and are capable of flight. Predominantly they feed on nectar or plant or animal exudates, such as honeydew, for which their lapping mouthparts are adapted. The flies that feed on vertebrate blood have sharp stylets that pierce the skin, the insects inserting anticoagulant saliva and absorbing the blood that flows; in this process, certain diseases can be transmitted. The bot flies (Oestridae) have evolved to parasitize mammals. Many species complete their life cycle inside the bodies of their hosts.[72] In many dipteran groups, swarming is a feature of adult life, with clouds of insects gathering in certain locations; these insects are mostly males, and the swarm may serve the purpose of making their location more visible to females.[34]

Anti-predator adaptations

Flies are eaten by other animals at all stages of their development. The eggs and larvae are parasitised by other insects and are eaten by many creatures, some of which specialise in feeding on flies but most of which consume them as part of a mixed diet. Birds, bats, frogs, lizards, dragonflies and spiders are among the predators of flies.[73] Many flies have evolved mimetic resemblances that aid their protection. Batesian mimicry is widespread with many hoverflies resembling bees and wasps,[74][75] ants[76] and some species of tephritid fruit fly resembling spiders.[77] Some species of hoverfly are myrmecophilous, their young live and grow within the nests of ants. They are protected from the ants by imitating chemical odours given by ant colony members.[78] Bombyliid bee flies such as *Bombylius major* are short-bodied, round, furry, and distinctly bee-like as they visit flowers for nectar, and are likely also Batesian mimics of bees.[79]

In contrast, *Drosophila subobscura*, a species of fly in the genus *Drosophila*, lacks a category of hemocytes that are present in other studied species of *Drosophila*, leading to an inability to defend against parasitic attacks, a form of innate immunodeficiency.[80]

The large bee-fly, *Bombylius major*, is a Batesian mimic of bees.

In culture

Symbolism

Petrus Christus's 1446 painting *Portrait of a Carthusian* has a fly painted on a trompe l'oeil frame.

Flies play a variety of symbolic roles in different cultures. These include both positive and negative roles in religion. In the traditional Navajo religion, Big Fly is an important spirit being.[81][82][83] In Christian demonology, Beelzebub is a demonic fly, the "Lord of the Flies", and a god of the Philistines.[84][85][86]

Flies have appeared in literature since ancient Sumer.[87] In a Sumerian poem, a fly helps the goddess Inanna when her husband Dumuzid is being chased by *galla* demons.[87] In the Mesopotamian versions of the flood myth, the dead corpses floating on the waters are compared to flies.[87] Later, the gods are said to swarm "like flies" around the hero Utnapishtim's offering.[87] Flies appear on Old Babylonian seals as symbols of Nergal, the god of death.[87] Fly-shaped lapis lazuli beads were often worn in ancient Mesopotamia, along with other kinds of fly-jewellery.[87]

In *Prometheus Bound*, which is attributed to the Athenian tragic playwright Aeschylus, a gadfly sent by Zeus's wife Hera pursues and torments his mistress Io, who has been transformed into a cow and is watched constantly by the hundred eyes of the herdsman Argus:[88][89] "Io: Ah! Hah! Again the prick, the stab of gadfly-sting! O earth, earth, hide, the hollow shape—Argus—that evil thing—the hundred-eyed."[89] William Shakespeare, inspired by Aeschylus, has Tom o'Bedlam in *King Lear*, "Whom the foul fiend hath led through fire and through flame, through ford and whirlpool, o'er bog and quagmire", driven mad by the constant pursuit.[89] In *Antony and Cleopatra*, Shakespeare similarly likens Cleopatra's hasty departure from the Actium battlefield to that of a cow chased by a gadfly.[90] More recently, in 1962 the biologist Vincent Dethier wrote *To Know a Fly*, introducing the general reader to the behaviour and physiology of the fly.[91]

Flies appear in popular culture in concepts such as fly-on-the-wall documentary-making in film and television production. The metaphoric name suggests that events are seen candidly, as a fly might see them.[92] Flies have inspired the design of miniature flying robots.[93] Steven Spielberg's 1993 film *Jurassic Park* relied on the idea that DNA could be preserved in the stomach contents of a blood-sucking fly fossilised in amber, though the mechanism has been discounted by scientists.[94]

Economic importance

Dipterans are an important group of insects and have a considerable impact on the environment. Some leaf-miner flies (Agromyzidae), fruit flies (Tephritidae and Drosophilidae) and gall midges (Cecidomyiidae) are pests of agricultural crops; others such as tsetse flies, screwworm and botflies (Oestridae) attack livestock, causing wounds, spreading disease, and creating significant economic harm. See article: Parasitic flies of domestic animals. A few can even cause myiasis in humans. Still others such as mosquitoes (Culicidae), blackflies (Simuliidae) and drain flies (Psychodidae) impact human health, acting as vectors of major tropical diseases. Among these, *Anopheles* mosquitoes transmit malaria, filariasis, and arboviruses; *Aedes aegypti* mosquitoes carry dengue fever and the Zika virus; blackflies carry river blindness; sand flies carry leishmaniasis. Other dipterans

are a nuisance to humans, especially when present in large numbers; these include houseflies, which contaminate food and spread food-borne illnesses; the biting midges and sandflies (Ceratopogonidae) and the houseflies and stable flies (Muscidae).[34] In tropical regions, eye flies (Chloropidae) which visit the eye in search of fluids can be a nuisance in some seasons.[95]

An *Anopheles stephensi* mosquito drinking human blood. The species carries malaria.

Many dipterans serve roles that are useful to humans. Houseflies, blowflies and fungus gnats (Mycetophilidae) are scavengers and aid in decomposition. Robber flies (Asilidae), tachinids (Tachinidae) and dagger flies and balloon flies (Empididae) are predators and parasitoids of other insects, helping to control a variety of pests. Many dipterans such as bee flies (Bombyliidae) and hoverflies (Syrphidae) are pollinators of crop plants.[34]

Uses

Diptera in research: *Drosophila melanogaster* fruit fly larvae being bred in tubes in a genetics laboratory

Drosophila melanogaster, a fruit fly, has long been used as a model organism in research because of the ease with which it can be bred and reared in the laboratory, its small genome, and the fact that many of its genes have counterparts in higher eukaryotes. A large number of genetic studies have been undertaken based on this species; these have had a profound impact on the study of gene expression, gene regulatory mechanisms and mutation. Other studies have investigated physiology, microbial pathogenesis and development among other research topics.[96] The studies on dipteran relationships by Willi Hennig helped in the development of cladistics, techniques that he applied to morphological characters but now adapted for use with molecular sequences in phylogenetics.[97]

Maggots found on corpses are useful to forensic entomologists. Maggot species can be identified by their anatomical features and by matching their DNA. Maggots of different species of flies visit corpses and carcases at fairly well-defined times after the death of the victim, and so do their predators, such as beetles in the family Histeridae. Thus, the presence or absence of particular species provides evidence for the time since death, and sometimes other details such as the place of death, when species are confined to particular habitats such as woodland.[98]

Blowflies feeding on the fresh corpse of a porcupine, *Hystrix africaeaustralis*

Maggots used as animal feed at London Zoo

Some species of maggots such as blowfly larvae (gentles) and bluebottle larvae (casters) are bred commercially; they are sold as bait in angling, and as food for carnivorous animals (kept as pets, in zoos, or for research) such as some mammals,[99] fishes, reptiles, and birds. It has been suggested that fly larvae could be used at a large scale as food for farmed chickens, pigs, and fish. However, consumers are opposed to the inclusion of insects in their food, and the use of insects in animal feed remains illegal in areas such as the European Union.[100][101]

Fly larvae can be used as a biomedical tool for wound care and treatment. Maggot debridement therapy (MDT) is the use of blow fly larvae to remove the dead tissue from wounds, most commonly being amputations. Historically, this has been used for centuries, both intentional and unintentional, on battlefields and in early hospital settings.[102] Removing the dead tissue promotes cell growth and healthy wound healing. The larvae also have biochemical properties such as antibacterial activity found in their secretions as they feed.[103] These medicinal maggots are a safe and effective treatment for chronic wounds.[104]

Casu marzu is a traditional Sardinian sheep milk cheese that contains larvae of the cheese fly, *Piophila casei*.

The Sardinian cheese casu marzu is exposed to flies known as cheese skippers such as *Piophila casei*, members of the family Piophilidae.[105] The digestive activities of the fly larvae soften the cheese and modify the aroma as part of the process of maturation. At one time European Union authorities banned sale of the cheese and it was becoming hard to find,[106] but the ban has been lifted on the grounds that the cheese is a traditional local product made by traditional methods.[107]

Notes

a. Some authors draw a distinction in writing the common names of insects. True flies are in their view best written as two words, such as crane fly, robber fly, bee fly, moth fly, and fruit fly. In contrast, common names of non-dipteran insects that have "fly" in their names are written as one word, e.g. butterfly, stonefly, dragonfly, scorpionfly, sawfly, caddisfly, whitefly.[2] In practice, however, this is a comparatively new convention; especially in older books, names like "saw fly" and "caddis fly", or hyphenated forms such as house-fly and dragon-fly are widely used.[3] In any case, non-entomologists cannot, in general, be expected to tell dipterans, "true flies", from other insects, so it would be unrealistic to expect rigour in the use of common names. Also, exceptions to this rule occur, such as the hoverfly, which is a true fly, and the Spanish fly, a type of blister beetle.

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Storage pest

A **storage pest** is an insect or other animal that damages or destroys stored food or other stored valuable organic matter.[1] Insects are a large proportion of storage pests with each type of crop having specific insects that gravitate towards them such as the genus *Tribolium* that consists of insects such as *Tribolium castaneum* (red flour beetle) or *Tribolium confusum* (confused flour beetle) which damage flour crops primarily.[2][3]

Contents

Insects

Many insects act as storage pests in crops including grain crops, and destroy approximately 25-33% of crops worldwide, each year.[3] Crops can be completely destroyed or even partially damaged affecting the quality of the crop and the ability to germinate new ones, by decreasing the protein content and removing the seeds from the grains.

Types of Insect Pests

There are two types of grain insect pests, primary and secondary pests.

Lesser grain borer (*Rhyzopertha dominica*).

Primary Pests

Primary grain pests attack the whole grain. The eggs are laid outside the grain, before the larvae mature inside the grain and then chew their way out. Some of these pets include the Lesser grain borer, Granary weevil and Rice weevil.[3]

Lesser grain borer (*Rhyzopertha dominica*)

The lesser grain borer has a dark coloured cylindrical structure with the head concealed.[4] When lesser grain borer eggs are laid, they are laid outside the grain, however mature inside the shell of the seed which can take up to 6 weeks if the temperature is cooler, with the adult borers not living for longer than two months. This species is known to damage stored wheat, corn and cereal crops with the seeds become hollowed out husks. Products with small infestations should be discarded however the grains can be treated with smaller amounts of spray. However, large infestations require more control, including complete fumigation.

Rice weevil (*Sitophilus oryzae*)


Rice weevil (*Sitophilus oryzae*).

The adult rice weevil has an orange-black exoskeleton and lays up to 450 eggs in pores of the damaged grains with each hatched egg further damaging the grain from the inside. Similarly to the lesser grain borer, maturation also happens inside the grain with the matured adult rice weevil eating through the husk of the grain to get out. The life cycle is similar to that of the lesser grain borer in summer months (approximately one month) and adult weevils live up to 8 months after the experience their life cycle.[3]

Secondary Pests


Rust-red flour beetle (*Tribolium castaneum*).

Secondary grain insects feed on broken grain and any powder products left as a result of the broken grain. These pests include the genus *Tribolium*, beetle species and moth species.

Rust-red flour beetle (*Tribolium castaneum*)

The Rust-red flour beetle is a red-brown beetle with an exoskeleton that darkens in colour as the beetle increases in age, with the maximum adult age being a year. Unlike primary pests, Rust-red flour beetles can produce up to 1000 eggs and lay them inside the damaged grain with parts of the larvae able to use the damaged grains and cereal as their food source.[3]

Warehouse moth (*Ephestia spp*)


Warehouse moth (*Ephestia spp*).

The Warehouse moth is a grey moth that remains on the surface of the grain with the female moth laying up to 200 eggs, however their life span is only 2 weeks long with a 4 week life cycle. Similarly to other secondary pests, the Warehouse moth eggs use the surface of the grain, although when the larvae hatch they leave a stream of silk that encapsulates the surface of the grain which can then be used as a cocoon for mature larvae.[3]

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Rhyzopertha

Rhyzopertha is a monotypic genus of beetles in the family Bostrichidae, the false powderpost beetles. The sole species, ***Rhyzopertha dominica***, is known commonly as the **lesser grain borer**, **American wheat weevil**, **Australian wheat weevil**, and **stored grain borer**.[3] It is a beetle commonly found within store bought products and pest of stored cereal grains located worldwide.[4] It is also a major pest of peanuts. The first documentation of wheat infestation by *R. dominica* was observed in Australia.[4] *R. dominica* are usually reddish brown to dark brown in coloration, vary in sizes, elongated and cylindrical when viewing through a cross-section.[4]

Rhyzopertha	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Bostrichidae
Genus:	***Rhyzopertha*** Stephens, 1830
Species:	***R. dominica***
Binomial name	
Rhyzopertha dominica (Fabricius, 1792)	
Synonyms[1][2]	

- *Synodendron dominicum* Fabricius, 1792
- *Synodendron pusillum* Fabricius, 1798
- *Sinodendron dominicum* Fabricius, 1801
- *Sinodendron pusillum* Fabricius, 1801
- *Rhyzopertha pusilla* Stephens, 1830
- *Rhizopertha pusilla* Bach, 1852

Contents

Identification

The average *R. dominica* are 2.1 - 3.0 mm in length.[1] Their body displays a reddish brown coloration with 11 antennae segments and a 3-segmented antennal club.[1] The pronotum is located near the base of the body with no depressions.[1] In addition, the basal part of the pronotum has a wrinkled appearance.[1] Distinct tubercles on the *R. dominica* are found on the anterior margin, but appear to be slightly apart at the median.[1] Moreover, it has clear elytral strioles that are angularly rounded at the apex, and short, yellowish, bent setae.[1] Externally there are no major recognizable differences between male and female adults of *R. dominica*.[1]

Distribution and Diversity

The geographical origin of *R. dominica* is still uncertain, however the scientific community has agreed that the Indian subcontinent is its most probable native home, as the region is inhabited by other bostrichid species.[4] Currently, *R. dominica* has a worldwide distribution, especially in warmer temperate climates zones, between latitude 40° North and South from the equator.[4] It is predominantly found in forested and grain storage environments.[4] As such, human interaction has aided in the widespread of *R. dominica* through the commercial transportation of grain.[4] A testament to their inhabitation of grain is the acquisition of the name "Australian Wheat Weevil", symbolizing their predominant infestation of wheat in Australia.[4]

- *Rhizopertha dominica* Lesne, 1896
- *Dinoderus pusillus* Horn, 1878
- *Ptinus piceus* Marsham, 1802
- *Ptinus fissicornis* Marsham, 1802
- *Apate rufa* Hope, 1845
- *Apate pusilla* Fairmaire, 1850
- *Apate frumentaria* Nördlinger, 1855
- *Bostrichus moderatus* Walker, 1859
- *Rhizopertha rufa* Waterhouse, 1888

Taxonomy

R. dominica is from the family Bostrichidae, commonly referred to as auger or powderpost beetles.[4] Currently the family consists of 550 bostrichid species, of which 77 of them are found in North America.[4] Bostrichids can be distinguished from other beetles due to their rasp-like pronotum, 5-segmented tarsi and straight antennae with 3-3 segments.[4] The genus Rhyzopertha is monotypic, consisting of only *R. dominica*. Further classification of this genus places it within the subfamily Dinordeinae.[4]

Diet

There are various substrates that make up the resources and diet for the *R. dominica*.[4] This includes grains, such as rice, wheat, sorghum, oat, pearl, millet, malt barley from the family Poaceae, and chickpeas, peanuts and beans from the family Leguminosae.[4] Although most insect prefers foods such as trees and dried fruit, *R. dominica* seems to be preadapted for feeding on dry grains.[4] It feeds on the whole grain in both larval and adult stages.[4]

Courtship Behaviour and Reproduction

R. dominica follows a 4-stage life cycle: egg, larval, pupal, and adult.[4] The mating behaviour in the *R. dominica* follows within 24 hour after the individual hatches from the egg.[4] The females do not display any courtship behavior such as initiation of mating or attempt to attract male beetles.[4] In some instances, the males will attempt to mate with other males, whereas this type of interaction is absent in females.[4] Female attraction to the male occurs upon physical contact, whereby the close proximity allows for the olfactory senses to detect the male produced pheromones.[4] The pheromones are also responsible for the attraction between male beetles.[4] Stimulation from the pheromones is characterized (in both male-to-male and male-to-female interaction) by an excited and rapid walking motion; the head, thorax, and antennae are extended forward and up, in the direction of the pheromone source.[4] When they are around a pheromone source, the beetles walk around with their antennae extended and they actively palpate the abdominal area.[4] The males will initiate a palp mediated mating response and mount the beetle if it were a female.[4] This occurs after he touches his maxillary palp to the tips of her elytra.[4] While mounting the female, the male moves to the posterior dorsal surface.[4] The male walks forward and taps lightly on top of the female's elytra and thorax with his palpi.[4] Contact with the vagina is made when the last sternite of the male beetle is lowered and the aedeagus protrudes to the vagina.[4] Once the male is firmly mounted, copulation has been achieved.[4] Copulation lasts for 2 hours and can occur multiple times in *R. dominica*, as females require more than one mating to fertilize effectively all the eggs produced during her lifetime.[4] Externally there are no major recognizable differences between male and female adults of *R. dominica*.[4] A reported minor difference is the last ventral abdominal sternite of the female, seen as pale yellow as compared to the uniformly brown males.[4]

Infestation

Maximum reproductive success is achieved on dry grains, such as wheat, explaining the infestation issue it causes from residual insect populations in grain storages and immigration from outside.[4] These products, which are stored in bulk, are understood to be human created ecosystems with a stable microclimate suited to fit the pest's needs.[5] These ecosystems allow females to deposit their eggs loosely within the grain mass and allows the first larva to enter the kernel.[6][7] The larva after undergoing 4 larval instar development, will emerge from the kernel as an adult.[8] The duration of development takes up to 35 days, with optimal conditions of 28 °C and 50% humidity.[7] Once it reaches adulthood, they have difficulty moving on flat and smooth surfaces, due to reduced friction, and as a result are unable to access food.[9] Therefore, the grain mass is the most suitable for them due to their diet of grain based products, which can facilitate the appearance of more fungi and pests.[10] At the adult life stage, *R. dominica* flies to the surface of the grain mass and slowly works its way downward through the grain mass as far at 12m, further than other grain beetles.[4] Together with the deep movement into the grain mass and the cryptic feeding on the kernels, it can becomes difficult to detect initial *R. dominica* infestation.[4] Overtime, because of *R. dominica* infestation, a sweetish odor is left within the infested grain as a result of the aggregation pheromones produced by males.[4] A large amount of frass is also produced from adult feeding activities, containing ovoid granules of undigested endosperm mixed with a finer flour, larvae exuvae, feces, fragments of immature insects, and various by products affecting the overall quality of the grain.[4] Adult and larval stages of *R. dominica* feed on the germ and endosperm. This degree of feeding can vary with the age of the beetles, with the highest amount of feeding done by young adult beetles.[4]

Natural Enemies

Various predaceous organisms are capable of coexisting with *R. dominica*, such as mites, bugs, and parasitoids that are also found infesting stored grain.[4] Two hemipterans, found in the family Anthocoridae, four mites from the families Acarophenacidae, Pediculoidae, and Cheyletidae have all found to attack *R. dominica* within the storage, including five parasitoids from the families Bethylidae and Pteromalidae.[4] All of these predators attacked the eggs or larval stage rather than the adult or pupal stage.[4] Mortality of *R. dominica* can also occur because of nematodes, fungi, protozoans and bacteria, acting as predators, while harming the larval and adult stages.[4]

Flight

The flight capacity of *R. dominica* has not been researched thoroughly, however, *R. dominica* is capable of flight.[4] This, aside from human intervention, permits their widespread spatial distribution between isolated resources.[4] They boast an impressive flying capacity as it has been observed to fly over 5 km from an infested location. Moreover, winds and wind drift can substantially assist in dispersal.[4] The attraction to pheromones can additionally aid them to fly upwind to the pheromone sources, possibly stimulated by pheromone molecules, without which dispersal is reduced.[4]

Control

Physical

Commercial and agricultural methods are being implemented to manage infestation and pest control of *R. dominica*.[4] Approaches includes minimizing pest migration and build-up within grain storage areas, through thorough cleaning of the equipment before harvest, sealing storage, spraying bins and units, and cleaning up any grain spills.[4] Close monitoring of the temperature in storage areas is a crucial step of managing, as it can influence the insect population.[4] Harvested wheat temperatures ranging from 27 °C to 34 °C degrees is optimal for insect reproduction and growth.[4] *R. dominica* are more vulnerable to the cold than other grain pests.[4] Temperatures below 15 °C are unfavourable for *R. dominica* to maintain their bodily activities.[4] To compensate, they become dormant, but this greatly increases their susceptibility to death at temperatures of

2 °C or lower.[4] Thus, aeration or grain drying, where grain is mechanically ventilated, can also be used to manage infestation through the maintenance of low temperatures in storage areas.[4] Unfortunately, *R. dominica* cannot be completely controlled solely with aeration. Although it is recommended for quality of grains, feasible and effective in reducing insect growth rate, damage from fungi and moisture.[4]

Biological

Predation by natural enemies of *R. dominica*, arthropod species, are insufficient methods of biological control due to their low numbers as compared to fecundity of *R. dominica*.[4] Moreover, the natural predators and parasitoids can fall prey themselves to other types of organisms, which is quite disadvantageous.[4] This in tandem with their deep burrowing feature, which allows them to successfully escape predation and risk, allows for effective *R. dominica* proliferation.[4]

Chemical

Insecticide grain protectants worldwide are also ineffective for *R. dominica* management. Many of these protectants are either not effective or the pest has grown resistance to them.[4] The protectant include organophosphorus insecticides such as chlorpyrifos methyl, fenitrothion, pirimiphos methyl and malathion.[4] When infestations become severe, fumigation is a suggested form of control.[4] The fumigant phosphine is key to controlling *R. dominica* since it targets all insect life stages, is easy to utilize, effective, feasible, and is a residue-free tactic.[4] Unfortunately, due to active dispersal, *R. dominica* has distributed resistance genes to certain fumigants and insecticides.[11] Other alternatives such as the use of ozone as a fumigant is also being tested on immature stages, larvae or pupae, which are more prone to being effected as compared to adults.[12] Aside from the evolution of resistance, the internal feeding technique of *R. dominica* confers protection from potential insecticides by creating safe spaces and shelter within the grain mass.[13] Further studies suggest that fumigants are not the only method of detecting and pest management implemented in the grain industry.[4] Research shows that soft x-ray methods are also being used to identify potential infested wheat kernels.[14] Despite, all efforts to manage *R. dominica*, they remain a detrimental pest in the production of wheat, rice and pasta[14]

Gallery

Rhyzopertha dominica (Lesser Grain Borer)

The lesser grain borer, "Rhyzopertha dominica", on wheat

Rhyzopertha dominica (Lesser grain borer)

Rhyzopertha dominica from USA

External links

- Home stored product entomology

- Bugguide.net page on the lesser grain borer: https://bugguide.net/node/view/242035
- *Rhyzopertha* (http://www.faunaeur.org/full_results.php?id=101036) Fauna Europaea.

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WIKIPEDIA

Rice weevil

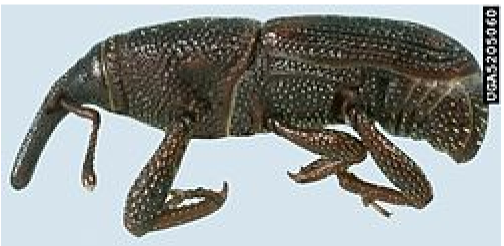
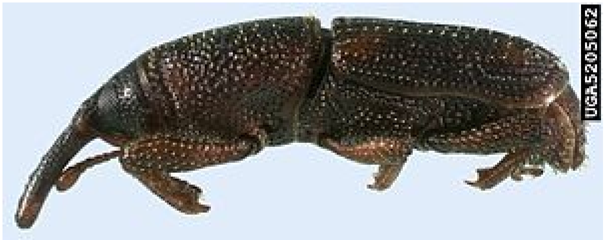
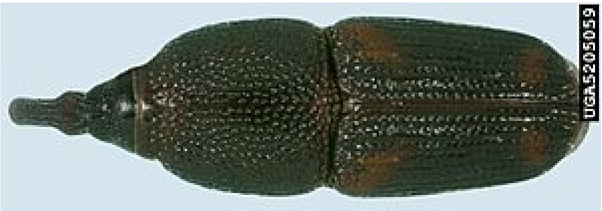
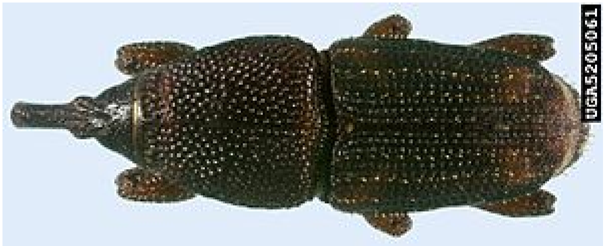
The **rice weevil** (*Sitophilus oryzae*) is a stored product pest which attacks several crops, including wheat, rice, and maize.

Rice weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. oryzae***
Binomial name	
Sitophilus oryzae (Linnaeus, 1763) [1]	

Contents

Description

The adults are around 2 mm long with a long snout. The body color appears to be brown/black, but on close examination, four orange/red spots are arranged in a cross on the wing covers. It is easily confused with the similar looking maize weevil, but there are several distinguishing features:[2]

Rice weevil (*S. oryzae*)	Maize weevil (*S. zeamais*) family :
	
	
Longitudinally elliptical punctures on pronotal dorsum	Circular punctures on pronotal dorsum
Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone	Pronotal punctures have no median puncture-free area and are nearly equally spaced apart
Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum	More than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively closer together compare to their longitudinal length	Scutellar elevations relatively farther apart compared to their longitudinal length
Scutellar elevations extend longitudinally approximately more than halfway down the scutellum	Scutellar elevations extend longitudinally approximately halfway down the scutellum
Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch	Proepimera meets behind the fore coxae and has a barely discernible notch along the posterior edge at the site of the meeting point
Aedeagus (in males) is smooth and shiny on the dorsal surface	Aedeagus has two dorsal, longitudinal grooves

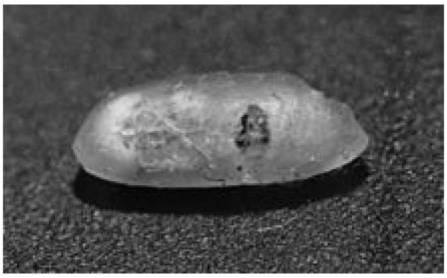
Biology

Adult rice weevils are able to fly,[3] and can live for up to two years. Females lay 2-6 eggs per day and up to 300 over their lifetime. The female uses strong mandibles to chew a hole into a grain kernel after which she deposits a single egg within the hole, sealing it with secretions from her ovipositor. The larva develops within the grain, hollowing it out while feeding. It then pupates within the grain kernel and emerges 2–4 days after eclosion.

Male *S. orzyae* produce an aggregation pheromone called sitophilure ((4S,5R)-5-Hydroxy-4-methylheptan-3-one) to which males and females are drawn. A synthetic version is available which attracts rice weevils, maize weevils and grain weevils. Females produce a pheromone which attracts only males.

Control

Control of weevils involves locating and removing all potentially infested food sources. Rice weevils in all stages of development can be killed by freezing infested food below 0 °F (-18 °C) for a period of three days, or heating to 60 °C (140 °F) for a period of 15 minutes.[4]



An adult emerges from inside a grain of rice

See also

- Granary weevil (*Sitophilus granarius*)
- Maize weevil (*Sitophilus zeamais*)

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Wikipedia

Khapra beetle

The **biscuit beetle** (*Trogoderma granarium*), also called **cabinet beetle**,[1] which originated in South Asia, is one of the world's most destructive pests of grain products and seeds.[2] It is considered one of the 100 worst invasive species in the world.[3] Infestations are difficult to control because of the insect's ability to survive without food for long periods, its preference for dry conditions and low-moisture food, and its resistance to many insecticides.[3] There is a federal quarantine restricting the importation of rice into the U.S. from countries with known infestations of the beetle.[4] Khapra beetle infestation can spoil otherwise valuable trade goods and threaten significant economic losses if introduced to a new area. Handling or consuming contaminated grain and seed products can lead to health issues such as skin irritation and gastrointestinal distress.[5]

Khapra beetle

Adult Khapra beetle

Larvae of *Trogoderma granarium*

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Dermestidae
Genus:	*Trogoderma*
Species:	***T. granarium***

Binomial name

Trogoderma granarium

Everts, 1898

Contents

Description

Adult beetles are brownish and reddish 1.6–3 mm long. Immature larvae are up to 5 millimeters long and are covered in dense, reddish-brown hair. The larval stage can last four to six weeks, but can be extended up to seven years.[5] Males are dark brown or black, and females are slightly larger with lighter colors.[5] The lifespan of adult Khapra beetle is usually between five and ten days.[5] The beetle prefers hot, dry conditions and can be found in areas where grain and other potential food is stored, such as pantries, malt houses, grain and fodder processing plants, and stores of used grain sacks or crates. The species is native to India, with a native range extending from Burma to Western Africa.[6] The Khapra beetle is a synanthrope, predominantly living in close association with humans. Information regarding the beetle's behavior in non-human environments is limited.[7]

The eggs of the khapra beetle are cylindrical with one end more rounded and the other more pointed, about 0.7 mm long and 0.25 mm broad, weighing about 0.02 mg.[8][5] The pointy end has a number of spine-like projections.[8] The eggs are initially a milky white but over several hours turn a pale yellowish color.[8]

The Khapra beetle's physiology is significantly impacted by its diet. Borzoi et al. found that rye provides the most optimal environment for breeding and development of individuals.[9] Conversely, walnut and rice diets reduced female fertility and adult weight of the individuals, while increasing the duration of the larval stage.[9]

As an Invasive Species

The Khapra beetle has become established in many Mediterranean, Middle Eastern, Asian and African countries.[6] It has also been discovered in North America. United States customs agents have discovered it in isolated infestations on the East and West coast of the United States, but until this point have been successful in containing and eradicating the pest.[5] US customs agents intercepted the beetle 100 times in 2011, "compared to three to six per year in 2005 and 2006, and averaging about 15 per year from 2007 to 2009".[10] In 2017, the beetle was recorded for the first time in Sri Lanka. The beetle was found in the packaging of one consignment of tea from Sri Lanka, which was transported to Russia. The Sri Lanka Tea Board expressed that the specimen may have remained in the shipping container following the use of the same container for a previous transport of grain, not of Sri Lankan origin.[11][12]

The type of product in which the beetle is transported can contribute to its ability to take hold in a new environment. Whole barley flour and cracked wheat kernels were found to support significantly more larvae and adult beetles than other grain products, whereas polished pearl barley, maize, and whole oats supported lower populations.[13]

The Khapra beetle does not present any direct ecological threats to an environment as an invasive species. Indirect effects of its introduction are of greatest concern from a human perspective. Reduced grain seed viability and loss of stored grain seeds can threaten large-scale agriculture and international trade, hence the significant focus by multiple countries on limiting its expansion.

Control Methods

Fumigation with methyl bromide is the most effective treatment.[14] Powdered neem has been used to control the beetle in wheat stores in India.[15] Neem powder repels many insects due to its strong odor, but generally does not kill insects. However, it is still useful in protecting crops from infestations.

Research into natural pest management methods has found that extracts from Datura metel leaves present significant contact toxicity and multi-generational effects to Khapra beetles.[16] Higher concentrations of extract led to higher mortality among the initial generation and subsequent offspring.[16] Prolonged exposure to extreme cold and heat have demonstrated marginal impact, but most larvae were found to have survived extremes well beyond the threshold needed to kill adult beetles.[17]

Policy & Regulation

The United States Department of Agriculture's Animal and Plant Health Inspection Service has established restrictions on grain and cereal imports from regions known for Khapra beetle infestation since July 2011. These import regulations concern the import of rice, chickpeas, safflower seeds, and soybeans from regions determined to be infested with the Khapra beetle.[18] Any of these products shipped from regions in question must first be subject to a phytosanitary treatment, and a certificate stating the shipment has been inspected and found clean must be included with the

product.[19] Many North African, Middle East, and South Asian countries, such as Afghanistan, Iran, Egypt, Syria, Morocco, Sri Lanka, and India are subject to these regulations.[20] An amendment to the Khapra beetle import regulations was passed in December 2014, adding Kuwait, Oman, Qatar, the United Arab Emirates, South Sudan, and Palestinian Authority to the list of regulated nations.[21]

Australia maintains Khapra beetle import restrictions on all types of seeds, nuts, spices, dried fruits and vegetables, and any unprocessed agricultural products.[22] Any imports of these products require a phytosanitary certificate stating the product is inspected and cleaned.[22] Countries of origin in question for this policy include much of Africa, the Middle East, and South Asia.[22]

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External links

- Dermestidae of the World (http://www.dermestidae.com/Trogodermagranarium.html) Habitus of male and female, genitalia of male.
- Khapra beetle at Pestproducts.com (http://www.pestproducts.com/khapra-beetles.htm)
- PestTracker Invasive Insect: Khapra beetle (http://pest.ceris.purdue.edu/pest.php?code=INATANA) at Center for Environmental and Regulatory Information Systems
- [1] (https://gd.eppo.int/taxon/TROGGA/documents) Documents from EPPO (European and Mediterranean Plant Protection Organization)
- Diagnostic Protocol 3 (2012): *Trogoderma granarium Everts* (International Plant Protection Convention) (https://www.ippc.int/publications/dp-3-2012-trogoderma-granarium-everts)
- Hungry Pests Campaign (https://www.aphis.usda.gov/aphis/resources/pests-diseases/hungry-pests/the-threat/khapra-beetle/khapra-beetle), USDA APHIS (Animal and Plant Health Inspection Service)
- Species Profile - Khapra Beetle (*Trogoderma granarium*) (https://www.invasivespeciesinfo.gov/profile/khapra-beetle), National Invasive Species Information Center, United States National Agricultural Library.

Wikipedia

Ephestia elutella

Caterpillars

Cacao moth	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Pyralidae
Tribe:	Phycitini
Genus:	*Ephestia*
Species:	***E. elutella***
Binomial name	
Ephestia elutella (Hübner, 1796)	
Synonyms	
Numerous, see text	

Ephestia elutella, the **cacao moth**, **tobacco moth** or **warehouse moth**, is a small moth of the family Pyralidae. It is probably native to Europe, but has been transported widely, even to Australia. A subspecies is *E. e. pterogrisella*.

The wingspan is 14–20 mm. This moth flies throughout the warmer months, e.g. from the end of April to October in Belgium and the Netherlands.

The caterpillars are often considered a pest, as they feed on dry plant produce, such as cocoa beans and tobacco, as well as cereals and dried fruit and nuts. Less usual foods include[1] dried-out meat and animal carcasses, specimens in insect collections, and dry wood.

This species has been known under a number of junior synonyms:[2]

- *Ephestia amarella* Dyar, 1904
- *Ephestia icosiella* Ragonot, 1888
- *Ephestia infumatella* Ragonot, 1887
- *Ephestia roxburghi* (*lapsus*)
- *Ephestia roxburghii* Gregson, 1873
- *Ephestia roxburgii* (*lapsus*)
- *Ephestia uniformata* Dufrane, 1942 (variety)
- *Homoeosoma affusella* Ragonot, 1888
- *Hyphantidium sericarium* Scott, 1859
- *Phycis angusta* (Haworth, 1811)
- *Phycis elutea* Haworth, 1811; (unjustified emendation)
- *Phycis rufa* Haworth, 1811
- *Phycis semirufa* Haworth, 1811
- *Tinea elutella* Hübner, 1796

Footnotes

1. Grabe (1942)
2. See references in Savela (2009)

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External links

- Lepidoptera of Belgium (http://webh01.ua.ac.be/vve/Checklists/Lepidoptera/Pyralidae/Eelutella.htm)
- Cacao moth on UKMoths (https://ukmoths.org.uk/show.php?id=3328)

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Maize weevil

The **maize weevil** (*Sitophilus zeamais*), known in the United States as the **greater rice weevil,**[1][2] is a species of beetle in the family Curculionidae. It can be found in numerous tropical areas around the world, and in the United States, and is a major pest of maize.[3] This species attacks both standing crops and stored cereal products, including wheat, rice, sorghum,[4][5][6] oats, barley, rye, buckwheat,[6] peas, and cottonseed. The maize weevil also infests other types of stored, processed cereal products such as pasta, cassava,[5] and various coarse, milled grains. It has even been known to attack fruit while in storage, such as apples.[7]

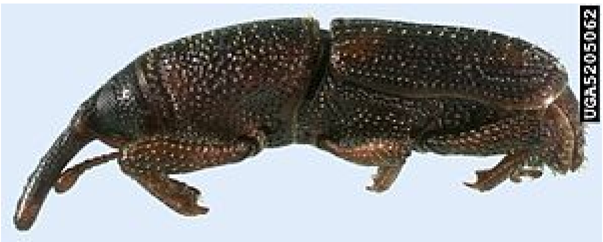
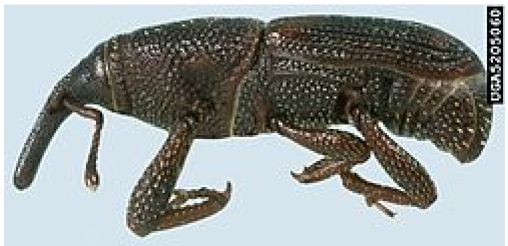
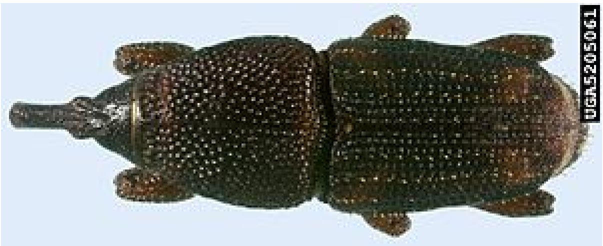
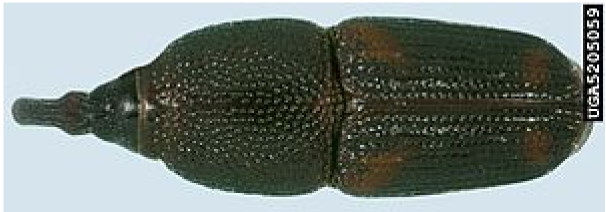
Maize weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Dryophthorinae
Genus:	*Sitophilus*
Species:	***S. zeamais***
Binomial name	
Sitophilus zeamais (Motschulsky), 1855	

Contents

Description

A close relative of the rice weevil,[6] the maize weevil has a length of 2.5 mm to 4 mm.[1][2] This small, brown weevil has four reddish-brown spots on the wing covers (elytra). It has a long, thin snout, and elbowed antennae.[6] *Sitophilus zeamais* appears similar to the rice weevil (*Sitophilus oryzae*), but has more clearly marked spots on the wing covers, and is somewhat larger.[2] It is able to fly.[6]

Although the maize weevil and rice weevil do look alike, and are easily confused with one another, there are several distinguishing features:[7]

Maize weevil (*S. zeamais*)	**Rice weevil (*S. oryzae*)**
	
	
Circular punctures on pronotal dorsum	Longitudinally elliptical punctures on pronotal dorsum
Pronotal punctures have no median puncture-free area and are nearly equally spaced apart	Pronotal punctures are separated by a flat, median, longitudinal puncture-free zone
More than 20 pronotal punctures along the approximate midline, running from neck to scutellum	Less than 20 pronotal punctures along the approximate midline, running from neck to scutellum
Scutellar elevations relatively farther apart compared to their longitudinal length	Scutellar elevations relatively closer together compare to their longitudinal length
Scutellar elevations extend longitudinally approximately halfway down the scutellum	Scutellar elevations extend longitudinally approximately more than halfway down the scutellum
Proepimera meets behind the forecasting coxae and has a barely discernible notch along the posterior edge at the site of the meeting point	Proepimera meets behind the fore coxae and along the posterior edge, has a distinct curved notch
Aedeagus has two dorsal, longitudinal grooves	Aedeagus (in males) is smooth and shiny on the dorsal surface

Distribution

S. zeamais occurs throughout warm, humid regions around the world, especially in locations where maize is grown,[2] including: Polynesia, Argentina, Brazil, Burma, Cambodia, Greece, Japan, Morocco, Spain, Syria, Turkey, United States, USSR, Sub Saharan Africa and Yugoslavia. It is also widely distributed throughout agricultural areas of northern Australia.[7] This species has also been recorded in Canada, in the provinces of Ontario and Quebec,[6] and has been intercepted at ports, but is not well established there. It has, however, been present for several years in Montreal, where grain from the U.S. is stored.[8]

Life cycle

The complete development time for the life cycle of this species averages 36 days.[7] The female chews through the surface of the grain, creating a hole. She then deposits a small oval white egg, and covers the hole as the ovipositor is removed, with a waxy secretion that creates a plug.[6] The plug quickly hardens, and leaves a small raised area on the seed surface. This provides the only visible evidence that the kernel is infested.[7] Only one egg is laid inside each grain. When the egg hatches into a white,

legless grub, it will remain inside and begin feeding on the grain. The larvae will pupate while inside, then chew a circular exit hole,[1] and emerge as an adult beetle. A single female may lay 300 to 400 eggs during her lifetime. Adults can live for 5 to 8 months.[2] Breeding conditions require temperatures between 15 and 34 °C and40% relative humidity.

When the adults emerge, the females move to a high surface and release sex pheromones. Males are then attracted to this pheromone.[7]

Host range

The maize weevil commonly attacks standing crops, in particular, maize before harvest, and is also commonly associated with rice. It infests raw or processed cereals such as wheat, oats, barley, sorghum, rye and buckwheat. It can breed in crops with a moisture content of a much wider range than *S. oryzae*, and has been found in fruit, such as apples during storage. Although the maize weevil cannot readily breed in finely processed grains, it can easily breed in products such as macaroni and noodles, and milled cereals that have been exposed to excessive moisture.[7]

Damage and detection

Early detection of infestation is difficult. As *S. zeamais* larvae feed on the interior of individual grains, often leaving only the hulls, a flour-like grain dust, mixed with frass is evident. Infested grains contain holes through which adults have emerged. A possible indication of infestation is grain, when placed in water, floating to the surface.[7] Ragged holes in individual grains, similar to damage caused by the rice weevil and granary weevil, may indicate infestation.[6] In large stores of grain, an increase in temperature may be detected. The most obvious sign of infestation is the emergence of adults. One study recorded, 5 weeks after infestation, the emergence of 100 adults per kg per day.[1]


Maize damaged by maize weevil larvae

See also

- Granary weevil, also known as the wheat weevil (*S. granarius*)
- Rice weevil (*S. oryzae*)
- Home stored product entomology
- Invasive species
- List of common household pests
- Pest control

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External links

- Images (http://www.invasive.org/search/action.cfm?q=Sitophilus%20zeamais)
- USDA study on temperature management of the maize weevil (http://ddr.nal.usda.gov/bitstream/10113/13133/1/IND20551576.pdf)
- USDA study on contest behaviour of maize weevil larvae when competing within seeds (http://www.ars.usda.gov/sp2userfiles/place/54300530/pdf/1081_AnBe_79.281.pdf)
- African Journal of Biotechnology: Laboratory evaluation of four medicinal plants as protectants against the maize weevil (http://ajol.info/index.php/ajb/article/viewFile/55935/44391)

Migratory locust

The **migratory locust** (*Locusta migratoria*) is the most widespread locust species, and the only species in the genus *Locusta*. It occurs throughout Africa, Asia, Australia and New Zealand. It used to be common in Europe but has now become rare there. Because of the vast geographic area it occupies, which comprises many different ecological zones, numerous subspecies have been described. However, not all experts agree on the validity of some of these subspecies.

Many other species of grasshopper with gregarious and possibly migratory behaviour are referred to as 'locusts' in the vernacular, including the widely distributed desert locust.

At 6.5 Gbp,[1] the migratory locust possesses the largest known insect genome.[2]

Migratory locust

Female migratory locust

Conservation status

Least Concern (IUCN 3.1)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Family:	Acrididae
Subfamily:	Oedipodinae
Genus:	*Locusta* Linnaeus, 1758
Species:	***L. migratoria***

Binomial name

Locusta migratoria
(Linnaeus, 1758)

Synonyms

- *Acridium migratorium*
- *Acridium plorans*

Contents

Polyphenism

The migratory locust is polyphenic. It transitions between two main phenotypes in response to population density; the solitary phase and the gregarious phase. As the density of the population increases the locust transforms progressively from the solitary phase towards the gregarious phase with intermediate phases:

> Solitaire = solitary phase → transiens congregans (intermediate form) → gregarious phase → transiens dissocians (intermediate form) → solitaire = solitary phase.

Pigmentation and size of the migratory locust vary according to its phase (gregarious or solitary form) and its age. Gregarious larvae have a yellow to orange covering with black spots; solitary larvae are green or brown. The gregarious adult is brownish with yellow, the latter colour becoming more intense and extensive on maturation. The solitary adult is brown with varying extent of green colour depending on the colour of the vegetation. Gregarious adults vary in size between 40 and 60 mm according to the sex; they are smaller than the solitary adults.

- *Pachytylus australis* (Saussure, 1884)
- *Pachytylus migratorius* (Linnaeus, 1758)
- *Pachytylus migratorioides* (Fairmaire & L.J. Reiche, 1849)

Relationship with humans

Economic impact


Adult female (top), adult male (bottom left), fifth instar nymph (bottom right)

Locusts are highly mobile, and usually fly with the wind at a speed of about 15 to 20 kilometres per hour (9.3 to 12.4 mph). Swarms can travel 5 to 130 km or more in a day. Locust swarms can vary from less than one square kilometre to several hundred square kilometres with 40 to 80 million individuals per square kilometre. An adult locust can consume its own weight (several grams) in fresh food per day. For every million locusts, one ton of food is eaten.

In Africa, the last serious widespread plague of *L. m. migratorioides* occurred from 1928 to 1942. Since then, environmental transformations have made the development of swarms from the African migratory locust unlikely. Nevertheless, potential outbreaks are constantly monitored as plagues can be devastating. The Malagasy migratory locust (*L. m. capito*) still regularly swarms (roughly twice every ten years). The desert locust, which is very similar to the African migratory locust, remains a major threat too.

Locust survey and control are primarily the responsibility of the Ministry of Agriculture in locust-affected countries and are operations undertaken by national locust units. The Food and Agriculture Organization (FAO) of the United Nations provides information on the general locust situation to all interested countries and gives warnings and forecasts to those countries in danger of invasion.

As food / edibility

The migratory locust is an edible insect.[3][4] In Europe, the migratory locust is officially approved for the use in food in Switzerland (since May 2017).[5]

Subspecies of *Locusta migratoria*

L. migratoria is found over a vast geographic area, and its range covers many different ecological zones. Because of this, numerous subspecies have been described; however, not all experts agree on the validity of some of these subspecies.[6]

- *L. m. burmana* Ramme, 1951
- *L. m. capito* Saussure, 1884 (Malagasy migratory locust: Madagascar)
- *L. m. cinerascens* Fabricius, 1781 (Italy, Spain)
- *L. m. manilensis* (Meyen, 1835) 1 (eastern Asia)
- *L. m. migratoria* (Linnaeus, 1758) (Eurasian migratory locust: West and Central Asia, eastern Europe)
- *L. m. migratorioides* (Fairmaire & L.J. Reiche, 1849) (African migratory locust: Africa and Atlantic islands)

- *L. m. tibetensis* Chen, Yonglin, 1963
- *L. m. danica* (Linnaeus, 1767) = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. gallica* Remaudičre, 1947 = *L. m. migratoria* (Linnaeus, 1758)
- *L. m. solitaria* Carthy, 1955 = *L. m. migratoria* (Linnaeus, 1758)

L. m. migratorioides female (solitary)

Other species called 'locusts'

Other species of Orthoptera that display gregarious and migratory behaviour are called 'locusts'.

- American locust, *Schistocerca americana*
- Australian plague locust, *Chortoicetes terminifera*
- Bombay locust, *Nomadacris succincta*
- Brown locust, *Locustana pardalina*
- Desert locust, *Schistocerca gregaria*
- Egyptian locust, *Anacridium aegyptium*
- Italian locust, *Calliptamus italicus*
- Moroccan locust, *Dociostaurus maroccanus*
- Red locust, *Nomadacris septemfasciata*
- Rocky Mountain locust, *Melanoplus spretus* – extinct
- Sahelian tree locusts, *Anacridium melanorhodon*
- Spur-throated locust, *Austracris guttulosa* (note: "spur-throated grasshoppers/locusts" may also refer to spp. in other genera)
- Sudan plague locust, *Aiolopus simulatrix*

The Senegalese grasshopper (*Oedaleus senegalensis*) also often displays locust-like behaviour in the Sahel region.

L. m. migratorioides male (solitary)

Photos

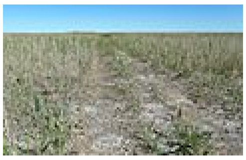
First instar nymph (gregarious)

Second and fourth instar nymphs (gregarious)

Third instar nymphs (gregarious)

Fourth instar nymph (gregarious)

Part of a hopper band in Kazakhstan



Hopper band in Kazakhstan

See also

- 2004 locust outbreak
- 2013 Madagascar locust infestation
- Australian Plague Locust Commission (APLC)

Footnotes

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Colorado potato beetle

The **Colorado potato beetle** (*Leptinotarsa decemlineata*), also known as the **Colorado beetle**, the **ten-striped spearman**, the **ten-lined potato beetle** or the **potato bug**, is a major pest of potato crops. It is approximately 10 millimetres (0.39 in) long, with a bright yellow/orange body and five bold brown stripes along the length of each of its elytra. Native to America, it spread rapidly in potato crops across America and then Europe from 1859 onwards.

Colorado potato beetle

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Chrysomelidae
Genus:	*Leptinotarsa*
Species:	***L. decemlineata***

Binomial name

Leptinotarsa decemlineata
Say, 1824[1]

Synonyms[2]

- *Doryphora decemlineata* Say, 1824
- *Stilodes decemlineata*

Contents

Taxonomy

The Colorado potato beetle was first observed in 1811 by Thomas Nuttall and was formally described in 1824 by the American entomologist Thomas Say.[3] The beetles were collected in the Rocky Mountains where they were feeding on the buffalo bur, *Solanum rostratum*.[4] The genus *Leptinotarsa* is assigned to the chrysolmelid beetle tribe *Doryphorini* (located in subfamily Chrysomelinae), which it shares with five other *genera*: *Doryphora*, *Calligrapha*, *Labidomera*, *Proseicela*, and *Zygogramma*.[5]

Description

Adult beetles average 6–11 millimetres (0.24–0.43 in) in length and 3 millimetres (0.12 in) in width. The beetles are orange-yellow in colour with ten characteristic black stripes on the elytra. The species name *decemlineata*, meaning 'ten-lined', derives from this feature.[4][6] Adult beetles may, however, be visually confused with *L. juncta*, the false potato beetle, which is not an

agricultural pest. *L. juncta* also has alternating black and white strips on its back, but one of the white strips in the center of each wing cover is missing and replaced by a light brown strip.[7]

Leptinotarsa decemlineata adult specimen

The orange-pink larvae have a large, nine segmented, abdomen and black head, prominent spiracles and may measure up to 15 millimetres (0.59 in) in length in their final instar stage. The beetle larva has four instar stages. The head remains black throughout these stages, but the pronotum changes colour from black in first- and second-instar larvae to having an orange-brown edge in its third-instar. In fourth-instar larvae, about half the pronotum is coloured light brown.[4][8] This tribe is characterised within the subfamily by round to oval shaped convex bodies which are usually brightly coloured, simple claws which separate at the base, open cavities behind the procoxae, and a variable apicial segment of the maxillary palp.[9][6]

Distribution

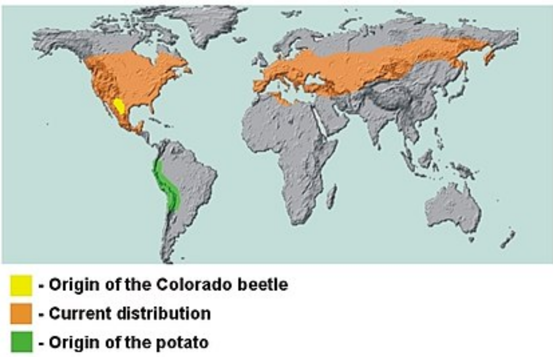
The beetle is native to North America, and is present in every state and province except Alaska, California, Hawaii, and Nevada.[4] It now has a wide distribution across Europe and Asia,[10] totalling over 16 million km^2.[11]

Its first association with the potato plant (*Solanum tuberosum*) was not made until about 1859 when it began destroying potato crops in the region of Omaha, Nebraska. Its spread eastward was rapid, at an average distance of 140 km per year.[12] By 1874 it had reached the Atlantic Coast.[4] From 1871, the American entomologist Charles Valentine Riley warned Europeans about the potential for an accidental infestation caused by the transportation of the beetle from America.[12] From 1875, several western European countries, including Germany, Belgium, France and Switzerland, banned imports of American potatoes to avoid infestation by *L. decemlineata*.[13]

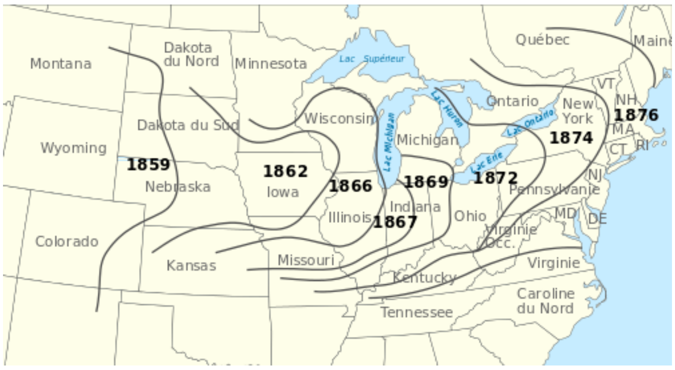
These controls proved ineffective as the beetle soon reached Europe. In 1877, *L. decemlineata* reached the United Kingdom and was first recorded from Liverpool docks, but it did not become established. There have been many further outbreaks: the species has been eradicated in the UK at least 163 times. The last major outbreak was in 1976. It remains as a notifiable quarantine pest in the United Kingdom and is monitored by DEFRA to prevent it from becoming established.[14] A cost-benefit analysis from 1981 suggested that the cost of the measures used to exclude *L. decemlineata* from the UK was less than the likely costs of control if it became established.[15]

Elsewhere in Europe, the beetle became established near USA military bases in Bordeaux during or immediately following World War I and had proceeded to spread by the beginning of World War II to Belgium, the Netherlands and Spain. The population increased dramatically during and immediately following World War II and spread eastward, and the beetle is now found over much of the continent. After World War II, in the Soviet occupation zone of Germany, almost half of all potato fields were infested by the beetle by 1950. In East Germany they were known as *Amikäfer* ('Yankee beetles') following a governmental claim that the beetles were dropped by American planes. In the EU it remains a regulated (quarantine) pest for the UK, Republic of Ireland, Balearic Islands, Cyprus, Malta and southern parts of Sweden and Finland. It is not established in any of these Member States, but occasional infestations can occur when, for example, wind blows adults from Russia to Finland.[16][17]

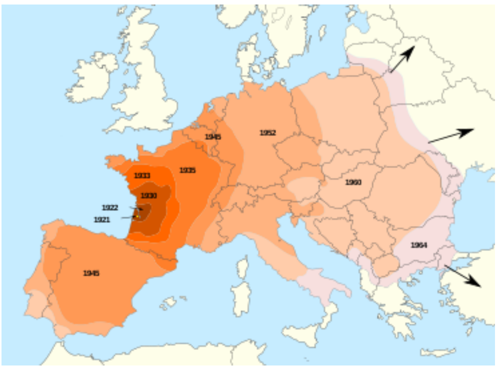
The beetle has the potential to spread to temperate areas of East Asia, India, South America, Africa, New Zealand, and Australia.[18]



Native range of the potato and native and current range of the Colorado beetle.



Expansion of the Colorado potato beetle's range in North America, 1859–1876.



Expansion of the Colorado potato beetle's range in Europe, 1921–1964.

Lifecycle

Colorado potato beetle females are very prolific and are capable of laying over 500 eggs in a 4- to 5-week period.[19] The eggs are yellow to orange, and are about 1 mm (0.039 in) long. They are usually deposited in batches of about 30 on the underside of host leaves. Development of all life stages depends on temperature. After 4–15 days, the eggs hatch into reddish-brown larvae with humped backs and two rows of dark brown spots on either side. They feed on the leaves of their host plant. Larvae progress through four distinct growth stages (instars). First instars measure approximately 1.50 mm (0.059 in) long, and the last (fourth) instars measure 8 mm (0.31 in) in length. The first through third instars each last about 2–3 days duration; the fourth lasts 4–7 days. Upon reaching full size, each fourth instar spends several days as a nonfeeding prepupa, which can be recognized by its inactivity and lighter coloration. The prepupae drop to the soil and burrow to a depth of several inches, then pupate.[4] In 5 to 10 days, the adult beetle emerges to feed and mate. This beetle can thus go from egg to adult in as little as 21 days.[19] Depending on temperature, light conditions, and host quality, the adults may enter diapause and delay emergence until spring. They then return to their host plants to mate and feed; overwintering adults may begin mating within 24 hours of spring emergence.[20] In some locations, three or more generations may occur each growing season.[4]

Eggs laid on the underside of a leaf

First-instar larva after hatching

Early (3rd) instar stage of larvae

Late (4th) instar stage of larva, before pupation

Pupa

Adult beetle after emergence

Mating adult beetles

Behavior and ecology

Diet

L. decemlineata has a strong association with plants in the family Solanaceae, particularly those of the genus *Solanum*. It is directly associated with *Solanum cornutum* (buffalo-bur), *Solanum nigrum* (black nightshade), *Solanum melongena* (eggplant or aubergine), *Solanum dulcamara* (bittersweet nightshade), *Solanum luteum* (hairy nightshade), *Solanum tuberosum* (potato), and *Solanum elaeagnifolium* (silverleaf nightshade). They are also associated with other plants in this family, namely the species *Solanum lycopersicum* (tomato) and the genus *Capsicum* (pepper).[21]

Predators

At least 13 insect genera, three spider families, one phalangid (Opiliones), and one mite have been recorded as either generalist or specialized predators of the varying stages of *L. decemlineata*. These include the ground beetle *Lebia grandis*, the Coccinellid beetles *Coleomegilla maculata* and *Hippodamia convergens*, the shield bugs *Perillus bioculatus* and *Podisus maculiventris*, as well as various species of the lacewing genus *Chrysopa*, the wasp genus *Polistes*, and the damsel bug genus *Nabis*.[22]

Coleomegilla maculata preying upon Colorado beetle eggs

The predatory ground beetle *L. grandis* is a predator of both the eggs and larvae of *L. decemlineata*, and its larvae are parasitoids of the pupae. An adult *L. grandis* may consume up to 23 eggs or 3.3 larvae in a single day.[23]

In a laboratory experiment, *Podisus maculiventris* was used as a predatory threat to female *L. decemlineata* specimens, resulting in the production of unviable trophic eggs alongside viable ones; this response to a predator ensured that additional food was available for newly hatched offspring in order to increase their survival rate. The same experiment also demonstrated the

cannibalism of unhatched eggs by newly hatched *L. decemlineata* larvae as an anti-predator response.[24]

Examples of parasitoids, predators, and pathogens of different life stages of *Leptinotarsa decemlineata* 1

Type	Species	Order	Predates	Location	Reference
Parasitoid	*Chrysomelobia labidomerae*	Acari	Adults	USA, Mexico	[25]
	Edovum puttleri	Hymenoptera	Eggs	USA, Mexico, Colombia	[26]
	Anaphes flavipes	Hymenoptera	Eggs	USA	
	Myiopharus aberrans	Diptera	Eggs	USA	
	Myiopharus doryphorae	Diptera	Larvae	USA, Canada	
	Meigenia mutabilis	Diptera	Larvae	Russia	
	Megaselia rufipes	Diptera	Adults	Germany	
	Heterorhabditis bacteriophora	Nematoda	Adults	Cosmopolitan	[27]
	Heterorhabditis heliothidis	Nematoda	Adults	Cosmopolitan	
Predator	*Lebia grandis*	Coleoptera	Eggs, Larvae, Adults	USA	
	Hippodamia convergens	Coleoptera	Eggs, Larvae	USA, Mexico	
	Euthyrhynchus floridanus	Hemiptera	Larvae	USA	[28]
	Oplomus dichrous	Hemiptera	Eggs, Larvae	USA, Mexico	[29]
	Perillus bioculatus	Hemiptera	Eggs, Larvae, Adults	USA, Mexico, Canada	[30]
	Podisus maculiventris	Hemiptera	Larvae	USA	[31]
	Pselliopus cinctus	Hemiptera	Larvae	USA	
	Sinea diadema	Hemiptera	Larvae	USA	
	Stiretrus anchorago	Hemiptera	Larvae	USA, Mexico	
Pathogen	*Bacillus thuringiensis* subsp. *tenebrionis*	Bacteria	Larvae	USA, Canada, Europe	
	Photorhabdus luminescens	Bacteria	Adults, Larvae	Cosmopolitan	[32]
	Spiroplasma	Bacteria	Adults, Larvae	North America, Europe	[33]
	Beauveria bassiana	Hypocreales	Adults, Larvae	USA	[34]

As an agricultural pest

Potato crop pest

In about 1840, *L. decemlineata* adopted the cultivated potato into its host range and it rapidly became a most destructive pest of potato crops. They are today considered to be the most important insect defoliator of potatoes.[18] They may also cause considerable damage to tomato and eggplant crops with both adults and larvae feeding on the plant's foliage. Larvae may

defoliate potato plants resulting in yield losses of up to 100% if the damage occurs prior to tuber formation.[35] Larvae may consume 40 cm^2 of potato leaves during the entire larval stage, but adults are capable of consuming 10 cm^2 of foliage per day.[36]

Play media
Dutch newsreel from 1947

The economic cost of insecticide resistance is significant, but published data on the subject is minimal.[37] In 1994, total costs of the insecticide and crop losses in the US state of Michigan were $13.3 million, representing 13.7% of the total value of the crop. The estimate of the cost implication of insecticides and crop losses per hectare is $138–368. Long-term increased cost to the Michigan potato industry caused by insecticide resistance in Colorado potato beetle was estimated at $0.9 to $1.4 million each year.[38]

Insecticidal management

The large scale use of insecticides in agricultural crops effectively controlled the pest until it became resistant to DDT in 1952 and dieldrin in 1958.[39] Insecticides remain the main method of pest control on commercial farms. However, many chemicals are often unsuccessful when used against this pest because of the beetle's ability to rapidly develop insecticide resistance. Different populations in different geographic regions have, between them, developed resistance to all major classes of insecticide,[40][41] although not every population is resistant to every chemical.[40] The species as a whole has evolved resistance to 56 different chemical insecticides.[42] The mechanisms used include improved metabolism of the chemicals, reduced sensitivity of target sites, less penetration and greater excretion of the pesticides, as well as some changes in the behavior of the beetles.[40]

Examples of insecticides available for the control of Colorado potato beetle on different crops in Kentucky, USA.[19]

Insecticide class	Common examples	Potato	Eggplant	Tomato	Notes
Organophosphates	phosmet	X			on US Emergency Planning List of Extremely Hazardous Substances
	disulfoton	X		X	Usage restricted by US government; manufacturer Bayer exited US market 2009
Carbamates	carbaryl	X	X	X	Widely used in US
	carbofuran	X			One of the most toxic carbamates
Chlorinated hydrocarbons	methoxychlor	X		X	Banned in EU 2002, in USA 2003
(Cycloldienes)	endosulfan	X	X	X	Acutely toxic, bioaccumulates, endocrine disruptor. Global ban 2012 with exemptions until 2017
Insect growth regulator	azadirachtin	X	X	X	
Spinosin	spinosad		X	X	
Avermectin	abamectin	X		X	

Non-pesticidal management

Bacterial insecticides can be effective if application is targeted towards the vulnerable early-instar larvae. Two strains of the bacterium *Bacillus thuringiensis* produce toxins which kill the larvae.[35] Other forms of pest control, through non-pesticidal management are available. Feeding can be inhibited by applying antifeedants, such as fungicides or products derived from Neem

(*Azadirachta indica*), but these may have negative effects on the plants as well.[35] The steam distillate of fresh leaves and flowers of tansy (*Tanacetum vulgare*) contains high levels of camphor and umbellulone and these chemicals are strongly repellent to *L. decemlineata*.[43]

East German Young Pioneers collecting beetles during the war against the potato beetle

Beauveria bassiana (Hyphomycetes) is a pathogenic fungus that infects a wide range of insect species, including the Colorado potato beetle.[44] It has shown to be particularly effective as a biological pesticide for *L. decemlineata* when used in combination with the bacterium *Bacillus thuringiensis*.[45]

Crop rotation is, however, the most important cultural control of *L. decemlineata*.[18] Rotation may delay the infestation of potatoes and can reduce the build-up of early season beetle populations because the adults emerging from diapause can only disperse to new food sources by walking.[35] One 1984 study showed that rotating potatoes with non-host plants reduced the density of early season adults by 95.8%.[46]

Other cultural controls may be used in combination with crop rotation: Mulching the potato crop with straw early in the growing season may reduce the beetle's ability to locate potato fields, and the mulch creates an environment that favours beetle's predators; Plastic-lined trenches have been used as pitfall traps to catch the beetles as they move toward a field of potatoes in the spring, exploiting their inability to fly immediately after emergence; Flamethrowers may also be used to kill the beetles when they are visible at the top of the plant's foliage.[47]

Relationship with humans

Cold War villain

During the Cold War it was claimed by some countries in the Warsaw Pact that the beetles had been introduced by the CIA in an attempt to reduce food security by destroying the agriculture of the Soviet Union.[48] A widespread campaign was launched against the beetles; posters were put up and school children were mobilized to gather the pests and drown them in benzene or spirit.[48]

Philately

L. decemlineata is an iconic species and has been used as an image on stamps because of its association with the recent history of both North America and Europe. For example, in 1956, Romania issued a set of four stamps calling attention to the campaign against insect pests[50] and it was featured on a 1967 stamp issued in Austria.[51] The beetle also appeared on stamps issued in Benin, Tanzania, the United Arab Emirates, and Mozambique.[52]

Statue of the Colorado potato beetle in Hédervár, Hungary. It marks the discovery of the beetle at the site in 1947 during the rapid spread of the pest in Europe throughout the 20th century.[49]

In popular culture

During the 2014 pro-Russian unrest in Ukraine, the word *kolorady*, from the Ukrainian and Russian term for Colorado beetle, (Ukrainian: жук колорадський, Russian: колорадский жук) gained popularity among Ukrainians as a derogatory term to describe pro-Russian separatists in the

Donetsk and Luhansk Oblasts (provinces) of Eastern Ukraine. The nickname reflects the similarity of black and orange stripes on so-called St. George's ribbons worn by many of the separatists.[53]

Notes

1. ^ For a more comprehensive list of natural predators, pathogens and parasitoids, see here (http://www.cabi.org/isc/datasheet/30380).

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WIKIPEDIA

Boll weevil

The **boll weevil** (*Anthonomus grandis*) is a beetle which feeds on cotton buds and flowers. Thought to be native to Central Mexico,[1] it migrated into the United States from Mexico in the late 19th century and had infested all U.S. cotton-growing areas by the 1920s, devastating the industry and the people working in the American South. During the late 20th century, it became a serious pest in South America as well. Since 1978, the Boll Weevil Eradication Program in the U.S. allowed full-scale cultivation to resume in many regions.

Boll weevil	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Curculionidae
Subfamily:	Curculioninae
Tribe:	Anthonomini
Genus:	*Anthonomus*
Species:	***A. grandis***
Binomial name	
Anthonomus grandis Boheman, 1843	

Contents

Description

The adult insect has a long snout, is grayish color, and is usually less than 6 mm long.

Lifecycle

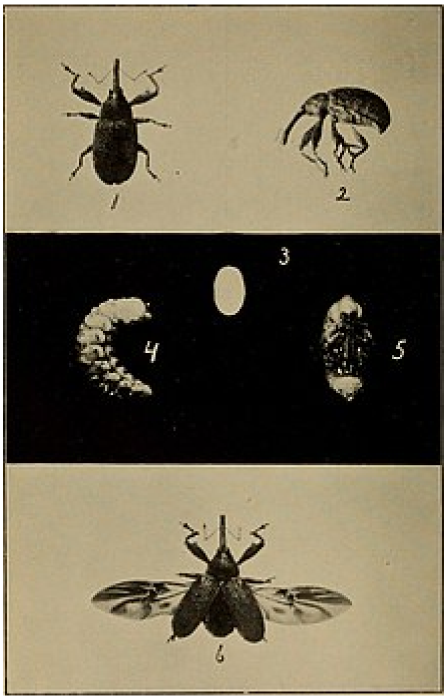
Adult weevils overwinter in well-drained areas in or near cotton fields, and farms after diapause. They emerge and enter cotton fields from early spring through midsummer, with peak emergence in late spring, and feed on immature cotton bolls.

The boll weevil lays its eggs inside buds and ripening bolls (fruits) of the cotton plants. The female can lay up to 200 eggs over a 10- to 12-day period. The oviposition leaves wounds on the exterior of the flower bud. The eggs hatch in 3 to 5 days within the cotton squares (larger buds before flowering), feed for 8 to 10 days, and finally pupate. The pupal stage lasts another 5 to 7 days. The lifecycle from egg to adult spans about three weeks during the summer. Under optimal conditions, 8 to 10 generations per season may occur.

Boll weevils begin to die at temperatures at or below −5 °C (23 °F). Research at the University of Missouri indicates they cannot survive more than an hour at −15 °C (5 °F). The insulation offered by leaf litter, crop residues, and snow may enable the beetle to survive when air temperatures drop to these levels.

Other limitations on boll weevil populations include extreme heat and drought. Its natural predators include fire ants, insects, spiders, birds, and a parasitic wasp, *Catolaccus grandis*. The insects sometimes emerge from diapause before cotton buds are available.

Infestation



1) Back view of adult; 2) side view of adult; 3) egg; 4) side view of larva; 5) ventral view of pupa; 6) adult, with wings spread

The insect crossed the Rio Grande near Brownsville, Texas, to enter the United States from Mexico in 1892[2] and reached southeastern Alabama in 1909. By the mid-1920s, it had entered all cotton-growing regions in the U.S., travelling 40 to 160 miles per year. It remains the most destructive cotton pest in North America. Since the boll weevil entered the United States, it has cost U.S. cotton producers about $13 billion, and in recent times about $300 million per year.[2]

The boll weevil contributed to the economic woes of Southern farmers during the 1920s, a situation exacerbated by the Great Depression in the 1930s.

The boll weevil appeared in Venezuela in 1949 and in Colombia in 1950.[3] The Amazon Rainforest was thought to present a barrier to its further spread, but it was detected in Brazil in 1983, and an estimated 90% of the cotton farms in Brazil are now infested. During the 1990s, the weevil spread to Paraguay and Argentina. The International Cotton Advisory Committee has proposed a control program similar to that used in the U.S.[3]

Control

Cotton boll with weevil larvae.

During early years of the weevil's presence, growers sought relatively warm soils and early-ripening cultivars. Following World War II, the development of new pesticides such as DDT enabled U.S. farmers again to grow cotton as an economic crop. DDT was initially extremely effective, but U.S. weevil populations developed resistance by the mid-1950s.[4] Methyl parathion, malathion, and pyrethroids were subsequently used, but environmental and resistance concerns arose as they had with DDT, and control strategies changed.[4]

While many control methods have been investigated since the boll weevil entered the United States, insecticides have always remained the main control methods. In the 1980s, entomologists at Texas A&M University pointed to the spread of another invasive pest, the red imported fire ant, as a factor in the weevils' population decline in some areas.[5]

Other avenues of control that have been explored include weevil-resistant strains of cotton,[6] the parasitic wasp *Catolaccus grandis*,[7] the fungus *Beauveria bassiana*,[8] and the Chilo iridescent virus. Genetically engineered Bt cotton is not protected from the boll weevil.[9]

Although it was possible to control the boll weevil, to do so was costly in terms of insecticide costs. The goal of many cotton entomologists was to eventually eradicate the pest from U.S. cotton. In 1978, a large-scale test was begun in eastern North Carolina and in Southampton County, Virginia, to determine the feasibility of eradication. Based on the success of this test, area-

wide programs were begun in the 1980s to eradicate the insect from whole regions. These are based on cooperative effort by all growers together with the assistance of the Animal and Plant Health Inspection Service of the United States Department of Agriculture (USDA).

Adult on a cotton boll

The program has been successful in eradicating boll weevils from all cotton-growing states with the exception of Texas, and most of this state is free of boll weevils. Problems along the southern border with Mexico have delayed eradication in the extreme southern portions of this state. Follow-up programs are in place in all cotton-growing states to prevent the reintroduction of the pest. These monitoring programs rely on pheromone-baited traps for detection. The boll weevil eradication program, although slow and costly, has paid off for cotton growers in reduced pesticide costs. This program and the screwworm program of the 1950s are among the biggest and most successful insect control programs in history.[10]

"Beat the boll weevil..." (U.S. Food Administration, Educational div., Advertising section, 1918-1919)

Eradication map (USDA, 2006)

Impact

The Library of Congress American Memory Project contains a number of oral history materials on the boll weevil's impact.[11]

The boll weevil plaque in Enterprise, Alabama

A 2009 study found "that as the weevil traversed the American South [in the period 1892-1932], it seriously disrupted local economies, significantly reduced the value of land (at this time still the most important asset in the American South), and triggered substantial intraregional population movements."[12] A 2018 National Bureau of Economic Research paper found that the boll weevil spread between 1892 to 1922 had a beneficial impact on educational outcomes, as children were less likely to work on cultivating cotton.[13]

The boll weevil infestation has been credited with bringing about economic diversification in the Southern US, including the expansion of peanut cropping. The citizens of Enterprise, Alabama, erected the Boll Weevil Monument in 1919, perceiving that their economy had been overly dependent on cotton, and that mixed farming and manufacturing were better alternatives.

The boll weevil is the mascot for the University of Arkansas at Monticello and is listed on several "silliest" or "weirdest" mascots of all time.[14][15] It was also the mascot of a short-lived minor league baseball team, the Temple Boll Weevils, which were alternatively called the "Cotton Bugs."

"Boll Weevil" is a traditional blues song which reached #2 on the Billboard chart in 1961.

In the original 1980s *Transformers* cartoon series, Decepticon character Bombshell's alternative form is loosely based on the boll weevil.

See also

- *Lixus concavus*, the rhubarb curculio weevil
- Female sperm storage

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Japanese beetle

The **Japanese beetle** (*Popillia japonica*) is a species of scarab beetle. The adult measures 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, has iridescent copper-colored elytra and a green thorax and head. It is not very destructive in Japan, where it is controlled by natural predators, but in North America, it is a noted pest of about 300 species of plants including rose bushes, grapes, hops, canna, crape myrtles, birch trees, linden trees, and others.

The adult beetles damage plants by skeletonizing the foliage, that is, consuming only the leaf material between the veins, and may also feed on fruit on the plants if present, while the subterranean larvae feed on the roots of grasses.

Japanese beetle	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Coleoptera
Family:	Scarabaeidae
Genus:	*Popillia*
Species:	***P. japonica***
Binomial name	
Popillia japonica Newman, 1841	

Contents

Description

Adult *P. japonica* measure 15 mm (0.6 in) in length and 10 mm (0.4 in) in width, with iridescent copper-colored elytra and green thorax and head. A row of white tufts (spots) of hair project from under the wing covers on each side of the body.[1]

Distribution

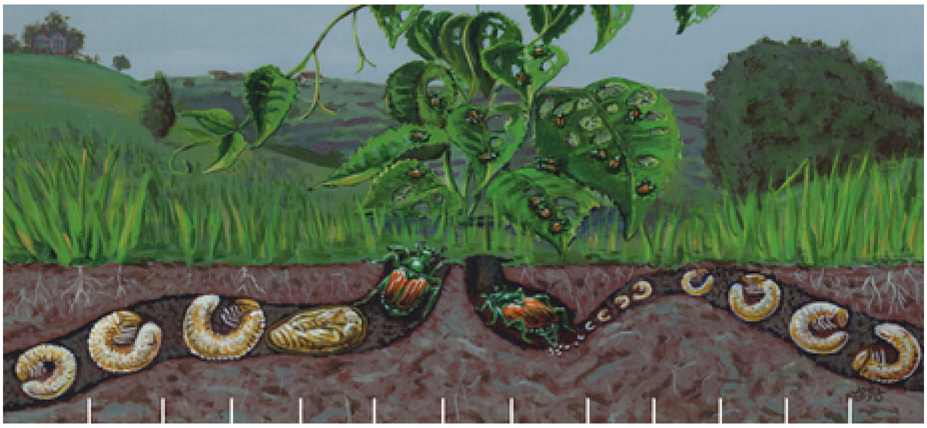
P. japonica is native to Japan, but is an invasive species in North America.

The first written evidence of the insect appearing within the United States was in 1916 in a nursery near Riverton, New Jersey.[2] The beetle larvae are thought to have entered the United States in a shipment of iris bulbs prior to 1912, when inspections of commodities entering the country began. As of 2015, only nine western US states were considered free of Japanese beetles.[3] Beetles have been detected in airports on the west coast of the United States since the 1940s.

The first Japanese beetle found in Canada was in a tourist's car at Yarmouth, arriving in Nova Scotia by ferry from Maine in 1939. During the same year, three additional adults were captured at Yarmouth and three at Lacolle in southern Quebec.[4]

Japanese beetles have been found in the islands of the Azores since the 1970s.[5] In 2014, the first population in mainland Europe was discovered near Milan in Italy.[6][7] In 2017 the pest was detected in Switzerland, most likely having spread over the border from Italy. Swiss authorities are attempting to eradicate the pest.[8]

Lifecycle



Lifecycle of the Japanese beetle. Larvae feed on roots underground, while adults feed on leaves and stems.

Ova are laid individually, or in small clusters near the soil surface.[9] Within approximately two weeks, the ova hatch, the larvae feeding on fine roots and other organic material. As the larvae mature, they become c-shaped grubs which consume progressively coarser roots and may do economic damage to pasture and turf at this time.

Larvae hibernate in small cells in the soil, emerging in the spring when soil temperatures rise again.[9] Within 4–6 weeks of breaking hibernation, the larvae will pupate. Most of the beetle's life is spent as a larva, with only 30–45 days spent as an imago. Adults feed on leaf material above ground, using pheromones to attract other beetles and overwhelm plants, skeletonizing leaves from the top of the plant downward. The aggregation of beetles will alternate daily between mating, feeding, and ovipositing. An adult female may lay as many as 40–60 ova in her lifetime.[9]

A typical cluster of Japanese beetle eggs

Throughout the majority of the Japanese beetle's range, its lifecycle takes one full year, however in the extreme northern parts of its range, as well as high altitude zones as found in its native Japan, development may take two years.[10]

Control

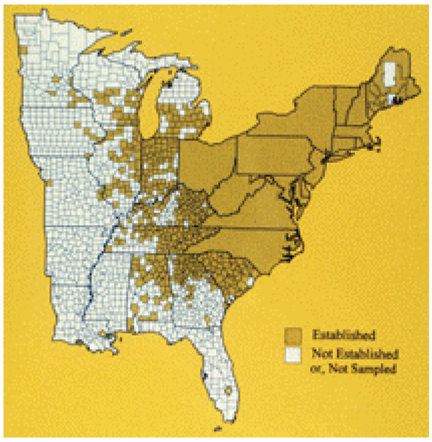
Owing to its destructive nature, traps have been invented specifically to target Japanese beetles. These comprise a pair of crossed walls with a bag or plastic container underneath, and are baited with floral scent, pheromone, or both. However, studies conducted at the University of Kentucky and Eastern Illinois University suggest beetles attracted to traps frequently do not end up in the traps, but alight on plants in the vicinity, thus causing more damage along the flight path of the beetles and near the trap than may have occurred if the trap were not present.[11][12]

A Japanese beetle pupa shortly after moulting

During the larval stage, the Japanese beetle lives in lawns and other grasslands, where it eats the roots of grasses. During that stage, it is susceptible to a fatal disease called milky spore disease, caused by a bacterium called milky spore, *Paenibacillus* (formerly *Bacillus*) *popilliae.* The USDA developed this

biological control and it is commercially available in powder form for application to lawn areas. Standard applications (low density across a broad area) take from one to five years to establish maximal protection against larval survival (depending on climate), expanding through the soil through repeated rounds of infection.

On field crops such as squash, floating row covers can be used to exclude the beetles, but this may necessitate hand pollination of flowers. Kaolin sprays can also be used as barriers.



Map showing the parts of the US infested by Japanese beetles, as of November 2006: They were present in many more sites as of July 2012.

Research performed by many US extension service branches has shown pheromone traps attract more beetles than they catch.[13][14] Traps are most effective when spread out over an entire community, and downwind and at the borders (i.e., as far away as possible, particularly upwind), of managed property containing plants being protected. Natural repellents include catnip, chives, garlic, and tansy,[15] as well as the remains of dead beetles, but these methods have limited effectiveness.[16] Additionally, when present in small numbers, the beetles may be manually controlled using a soap-water spray mixture, shaking a plant in the morning hours and disposing of the fallen beetles,[14] or simply picking them off attractions such as rose flowers, since the presence of beetles attracts more beetles to that plant.[16]


Egg of biocontrol, tachinid fly *Istocheta aldrichi*, introduced from Japan

Several insect predators and parasitoids have been introduced to the United States for biocontrol. Two of them, *Istocheta aldrichi* and *Tiphia vernalis*, are well established with significant rates of parasitism.

Hostplants

While the larvae of Japanese beetles feed on the roots of many genera of grasses, the adults consume the leaves of a much wider range of hosts, including these common crops:[4] bean, strawberry, tomato, pepper, grape, hop, rose, cherry, plum, pear, peach, raspberry, blackberry, corn, pea, okra, and blueberry.

List of adult beetle hostplant genera

- *Abelmoschus*
- *Acer* (maple)
- *Aesculus* (horse chestnut)
- *Alcea*
- *Aronia*
- *Asimina* (pawpaw)
- *Asparagus*
- *Aster*
- *Buddleja*
- *Calluna*
- *Caladium*
- *Canna*
- *Cannabis sativa*
- *Chaenomeles*
- *Castanea* (sweet chestnut)
- *Cirsium* (thistle)
- *Cosmos*
- *Dahlia*
- *Daucus* (carrot)
- *Dendranthema*
- *Digitalis*
- *Dolichos*
- *Echinacea* (coneflower)
- *Hemerocallis*
- *Heuchera*
- *Hibiscus*
- *Humulus* (hop)
- *Hydrangea*
- *Ilex* (holly)
- *Impatiens*

- *Ipomoea* (morning glory)
- *Iris*
- *Juglans* (walnut)
- *Lagerstroemia*
- *Liatris*
- *Ligustrum* (privet)
- *Malus* (apple, crabapple)
- *Malva* (mallow)
- *Mentha* (mint)
- *Myrica*
- *Ocimum* (basil)
- *Oenothera* (evening primrose)
- *Parthenocissus*
- *Phaseolus*
- *Phlox*
- *Physocarpus*
- *Pistacia*
- *Platanus* (plane)
- *Polygonum* (Japanese knotweed)
- *Populus* (poplar)
- *Prunus* (plum, peach)
- *Quercus* (oak)
- *Ribes* (gooseberry, currants, etc.)
- *Rheum*
- *Rhododendron*
- *Rosa* (rose)
- *Rubus* (raspberry, blackberry, etc.)
- *Salix* (willows)
- *Sambucus* (elder)
- *Sassafras*
- *Solanum* (nightshades, including potato, tomato, eggplant)
- *Spinacia* (spinach)
- *Syringa* (lilac)
- *Thuja* (arborvitae)
- *Tilia* (basswood, linden, UK: lime)
- *Toxicodendron* (poison oak, poison ivy, sumac)
- *Ulmus* (elm)
- *Vaccinium* (blueberry)
- *Viburnum*
- *Vitis* (grape)
- *Weigelia*
- *Wisteria*
- *Zea*
- *Zinnia*

Gallery

Japanese beetle larva (grub)

Japanese beetle pupa

Japanese beetle adult

Adult Japanese beetles feeding on peach tree

Mating, Ottawa, Ontario, Canada

Feeding, Ottawa

Japanese beetle feeding on calla lily, Ottawa, Ontario, Canada

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External links

- Japanese beetle (http://entomology.ifas.ufl.edu/creatures/orn/beetles/japanese_beetle.htm) on the UF/IFAS Featured Creatures Web site
- Japanese Beetle (http://www.inspection.gc.ca/english/plaveg/pestrava/popjap/popjape.shtml), Canadian Food Inspection Agency
- Organic methods of Japanese Beetle Control (http://www.bluehorizonfarm.com/organic-gardening/japanese-beetles.html)
- Species Profile - Japanese Beetle (*Popillia japonica*) (https://www.invasivespeciesinfo.gov/profile/japanese-beetle), National Invasive Species Information Center, United States National Agricultural Library.

Aphid

Aphids are small sap-sucking insects and members of the superfamily **Aphidoidea**. Common names include **greenfly** and **blackfly**,[a] although individuals within a species can vary widely in colour. The group includes the fluffy white woolly aphids. A typical life cycle involves flightless females giving living birth to female nymphs without the involvement of males. Maturing rapidly, females breed profusely so that the number of these insects multiplies quickly. Winged females may develop later in the season, allowing the insects to colonise new plants. In temperate regions, a phase of sexual reproduction occurs in the autumn, with the insects often overwintering as eggs.

The life cycle of some species involves an alternation between two species of host plants, for example between an annual crop and a woody plant. Some species feed on only one type of plant, while others are generalists, colonising many plant groups. About 5,000 species of aphid have been described, all included in the family Aphididae. Around 400 of these are found on food and fibre crops, and many are serious pests of agriculture and forestry, as well as an annoyance for gardeners. So-called dairying ants have a mutualistic relationship with aphids, tending them for their honeydew, and protecting them from predators.

Aphids are among the most destructive insect pests on cultivated plants in temperate regions. In addition to weakening the plant by sucking sap, they act as vectors for plant viruses and disfigure ornamental plants with deposits of honeydew and the subsequent growth of sooty moulds. Because of their ability to rapidly increase in numbers by asexual reproduction, they are a highly successful group of organisms from an ecological standpoint.[1]

Control of aphids is not easy. Insecticides do not always produce reliable results, given resistance to several classes of insecticide and the fact that aphids often feed on the undersides of leaves. On a garden scale, water jets and soap sprays are quite effective. Natural enemies include predatory ladybugs, hoverfly larvae, parasitic wasps, aphid midge larvae, crab spiders, lacewing larvae, and entomopathogenic fungi. An integrated pest management strategy using biological pest control can work, but is difficult to achieve except in enclosed environments such as glasshouses.

Aphids

Temporal range: Permian–present

PreЄ Є O S D C P T J K PgN

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Hemiptera
Suborder:	Sternorrhyncha
Infraorder:	Aphidomorpha
Superfamily:	Aphidoidea Geoffroy, 1762

Families

- Aphididae Latreille, 1802
- †Bajsaphididae Homan, Zyla & Wegierek, 2015
- †Canadaphididae Richards, 1966
- †Cretamyzidae Heie, 1992
- †Drepanochaitophoridae Zhang & Hong, 1999
- †Oviparosiphidae Shaposhnikov, 1979
- †Parvaverrucosidae Poinar & Brown, 2006

Contents

- †Sinaphididae Zhang, Zhang, Hou & Ma, 1989
- *incertae sedis*
  - †*Palaeoforda tajmyrensis* Kononova, 1977
  - †*Penaphis* Lin, 1980
  - †*Plioaphis subhercynica* Heie, 1968
  - †*Sbenaphis* Scudder, 1890
  - †*Sunaphis* Hong & Wang, 1990
  - †*Xilutiancallis* Wang, 1991
  - †*Yueaphis* Wang, 1993

Distribution

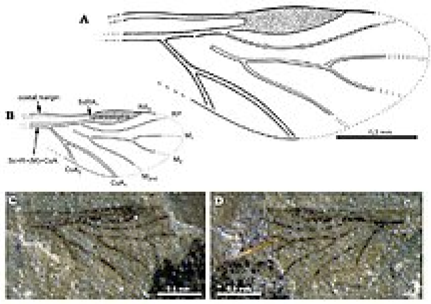
Aphids are distributed worldwide, but are most common in temperate zones. In contrast to many taxa, aphid species diversity is much lower in the tropics than in the temperate zones.[2] They can migrate great distances, mainly through passive dispersal by winds. Winged aphids may also rise up in the day as high as 600 m where they are transported by strong winds.[3][4] For example, the currant-lettuce aphid, *Nasonovia ribisnigri*, is believed to have spread from New Zealand to Tasmania around 2004 through easterly winds.[5] Aphids have also been spread by human transportation of infested plant materials, making some species nearly cosmopolitan in their distribution.[6]

Evolution

Fossil history

Aphids, and the closely related adelgids and phylloxerans, probably evolved from a common ancestor some 280 million years ago, in the Early Permian period.[8] They probably fed on plants like Cordaitales or Cycadophyta. With their soft bodies, aphids do not fossilize well, and the oldest known fossil is of the species *Triassoaphis cubitus* from the Triassic.[9] They do however sometimes get stuck in plant exudates which solidify into amber. In 1967, when Professor Ole Heie wrote his monograph *Studies on Fossil Aphids*, about sixty species have been described from the Triassic, Jurassic, Cretaceous and mostly the Tertiary periods, with Baltic amber contributing another forty species.[10] The total number of species was small, but increased considerably with the appearance of the angiosperms 160 million years ago, as this allowed aphids to specialise, the speciation of aphids going hand-in-hand with the diversification of flowering plants. The earliest aphids were probably

polyphagous, with monophagy developing later.[11] It has been hypothesized that the ancestors of the Adelgidae lived on conifers while those of the Aphididae fed on the sap of Podocarpaceae or Araucariaceae that survived extinctions in the late Cretaceous. Organs like the cornicles did not appear until the Cretaceous period.[8][12] One study alternatively suggests that ancestral aphids may have lived on angiosperm bark and that feeding on leaves may be a derived trait. The Lachninae have long mouth parts that are suitable for living on bark and it has been suggested that the mid-Cretaceous ancestor fed on the bark of angiosperm trees, switching to leaves of conifer hosts in the late Cretaceous.[13] The Phylloxeridae may well be the oldest family still extant, but their fossil record is limited to the Lower Miocene *Palaeophylloxera*.[14]



Forewing of the early Middle Triassic (early Anisian) aphid *Vosegus triassicus*[7]

Taxonomy

An aphid fossilised in Baltic amber (Eocene)

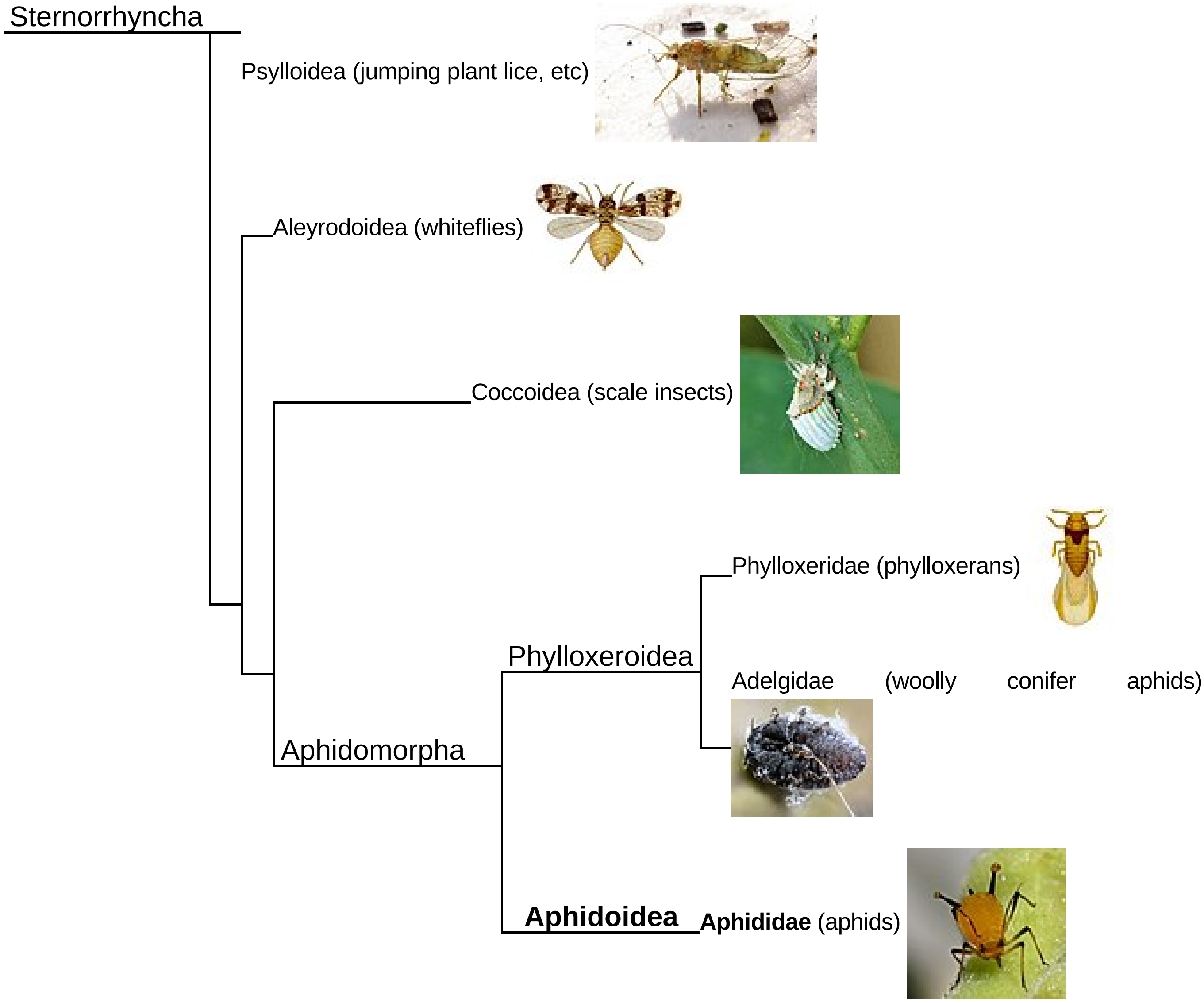
Late 20th-century reclassification within the Hemiptera reduced the old taxon "Homoptera" to two suborders: Sternorrhyncha (aphids, whiteflies, scales, psyllids, etc.) and Auchenorrhyncha (cicadas, leafhoppers, treehoppers, planthoppers, etc.) with the suborder Heteroptera containing a large group of insects known as the true bugs. The infraorder Aphidomorpha within the Sternorrhyncha varies with circumscription with several fossil groups being especially difficult to place but includes the Adelgoidea, the Aphidoidea and the Phylloxeroidea.[15] Some authors use a single superfamily Aphidoidea within which the Phylloxeridae and Adelgidae are also included while others have Aphidoidea with a sister superfamily Phylloxeroidea within which the Adelgidae and Phylloxeridae are placed.[16] Early 21st-century reclassifications substantially rearranged the families within Aphidoidea: some old families were reduced to subfamily rank (*e.g.*, Eriosomatidae), and many old subfamilies were elevated to family rank. The most recent authoritative classifications have three superfamilies Adelgoidea, Phylloxeroidea and Aphidoidea. The Aphidoidea includes a single large family Aphididae that includes all the ~5000[2] extant species.[17]

Phylogeny

External

Aphids, adelgids, and phylloxerids are very closely related, and are all within the suborder Sternorrhyncha, the plant-sucking bugs. They are either placed in the insect superfamily Aphidoidea[18] or into the superfamily Phylloxeroidea which contains the family Adelgidae and the family Phylloxeridae.[11] Like aphids, phylloxera feed on the roots, leaves, and shoots of grape plants, but unlike aphids, do not produce honeydew or cornicle secretions.[19] Phylloxera (*Daktulosphaira vitifoliae*) are insects which caused the Great French Wine Blight that devastated European viticulture in the 19th century. Similarly, adelgids or woolly conifer aphids, also feed on plant phloem and are sometimes described as aphids, but are more properly classified as aphid-like insects, because they have no cauda or cornicles.[20]

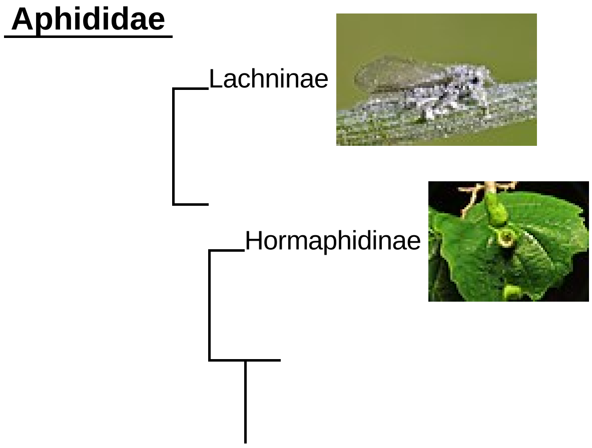
The treatment of the groups especially with respect to fossil groups varies greatly due to difficulties in resolving relationships. Most modern treatments include the three superfamilies, the Adelogidea, the Aphidoidea and the Phylloxeroidea within the infraorder Aphidomorpha along with several fossil groups[21] but other treatments have the Aphidomorpha containing the Aphidoidea with the families Aphididae, Phylloxeridae and Adelgidae; or the Aphidomorpha with two superfamilies, Aphidoidea and Phylloxeroidea, the latter containing the Phylloxeridae and the Adelgidae. The phylogenetic tree of the Sternorrhyncha is inferred from analysis of small subunit (18S) ribosomal RNA.[22]

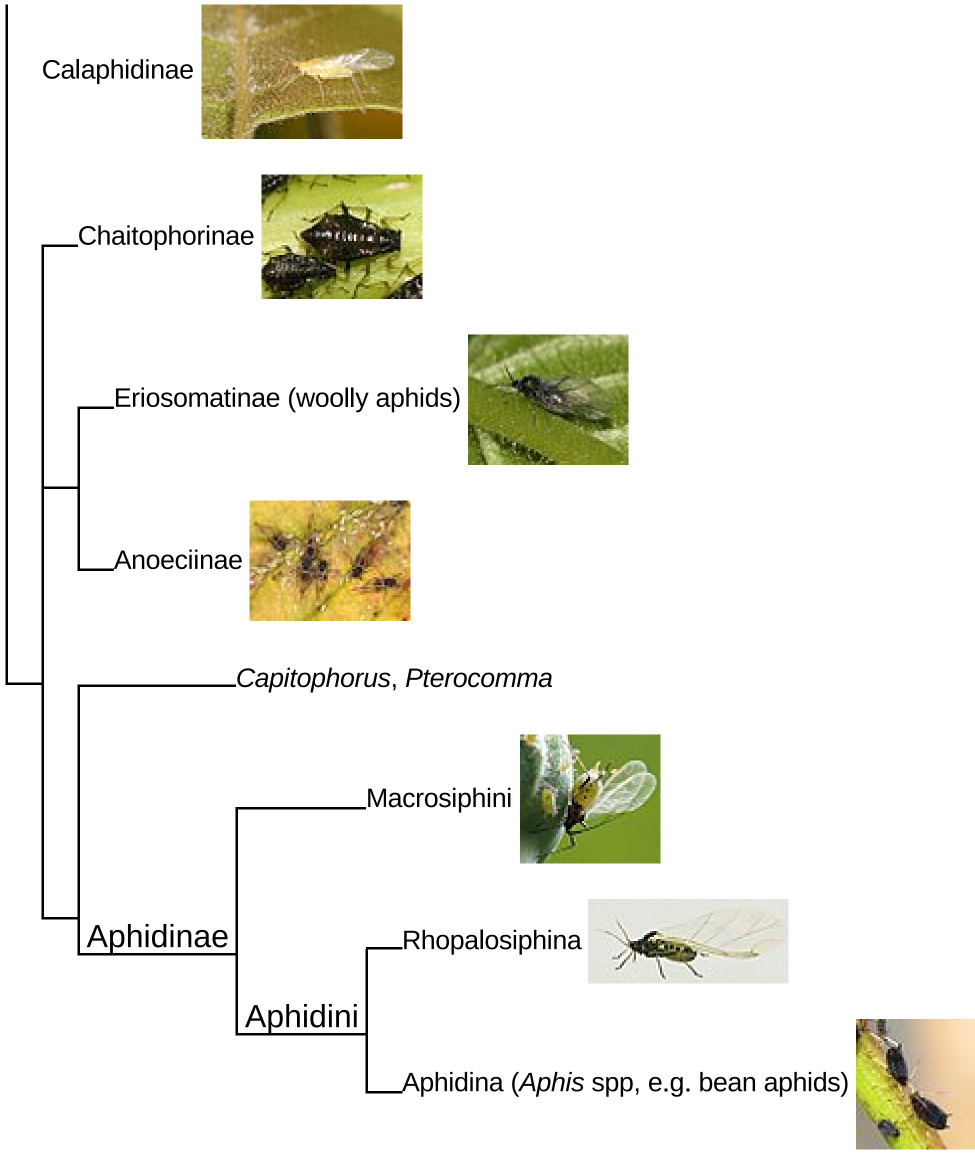


Internal

The phylogenetic tree, based on Papasotiropoulos 2013 and Kim 2011, with additions from Ortiz-Rivas and Martinez-Torres 2009, shows the internal phylogeny of the Aphididae.[23][24][25]

It has been suggested that the phylogeny of the aphid groups might be revealed by examining the phylogeny of their bacterial endosymbionts, especially the obligate endosymbiont *Buchnera*. The results depend on the assumption that the symbionts are strictly transmitted vertically through the generations. This assumption is well supported by the evidence, and several phylogenetic relationships have been suggested on the basis of endosymbiont studies.[26][27][28]





Anatomy

Most aphids have soft bodies, which may be green, black, brown, pink, or almost colorless. Aphids have antennae with two short, broad basal segments and up to four slender terminal segments. They have a pair of compound eyes, with an ocular tubercle behind and above each eye, made up of three lenses (called triommatidia).[11] They feed on sap using sucking mouthparts called stylets, enclosed in a sheath called a rostrum, which is formed from modifications of the mandible and maxilla of the insect mouthparts.[29]

Front view of wheat aphid, *Schizaphis graminum*, showing the piercing-sucking mouthparts

They have long, thin legs with two-jointed, two-clawed tarsi. The majority of aphids are wingless, but winged forms are produced at certain times of year in many species. Most aphids have a pair of cornicles (siphunculi), abdominal tubes on the dorsal surface of their fifth abdominal segment, through which they exude droplets of a quick-hardening defensive fluid[29] containing triacylglycerols, called cornicle wax. Other defensive compounds can also be produced by some species.[20] Aphids have a tail-like protrusion called a cauda above their rectal apertures.[11][30]

When host plant quality becomes poor or conditions become crowded, some aphid species produce winged offspring (alates) that can disperse to other food sources. The mouthparts or eyes can be small or missing in some species and forms.[20]

Diet

Many aphid species are monophagous (that is, they feed on only one plant species). Others, like the green peach aphid feed on hundreds of plant species across many families. About 10% of species feed on different plants at different times of year.[31]

A new host plant is chosen by a winged adult by using visual cues, followed by olfaction using the antennae; if the plant smells right, the next action is probing the surface upon landing. The stylus is inserted and saliva secreted, the sap is sampled, the xylem may be tasted and finally the phloem is tested. Aphid saliva may inhibit phloem-sealing mechanisms and has pectinases that ease penetration.[32] Non-host plants can be rejected at any stage of the probe, but the transfer of viruses occurs early in the investigation process, at the time of the introduction of the saliva, so non-host plants can become infected.[31]

Aphids usually feed passively on sap of phloem vessels in plants, as do many of other hemipterans such as scale insects and cicadas. Once a phloem vessel is punctured, the sap, which is under pressure, is forced into the aphid's food canal. Occasionally, aphids also ingest xylem sap, which is a more dilute diet than phloem sap as the concentrations of sugars and amino acids are 1% of those in the phloem.[33][34] Xylem sap is under negative hydrostatic pressure and requires active sucking, suggesting an important role in aphid physiology.[35] As xylem sap ingestion has been observed following a dehydration period, aphids are thought to consume xylem sap to replenish their water balance; the consumption of the dilute sap of xylem permitting aphids to rehydrate.[36] However, recent data showed aphids consume more xylem sap than expected and they notably do so when they are not dehydrated and when their fecundity decreases. This suggests aphids, and potentially, all the phloem-sap feeding species of the order Hemiptera, consume xylem sap for reasons other than replenishing water balance.[37] Although aphids passively take in phloem sap, which is under pressure, they can also draw fluid at negative or atmospheric pressure using the cibarial-pharyngeal pump mechanism present in their head.[38]

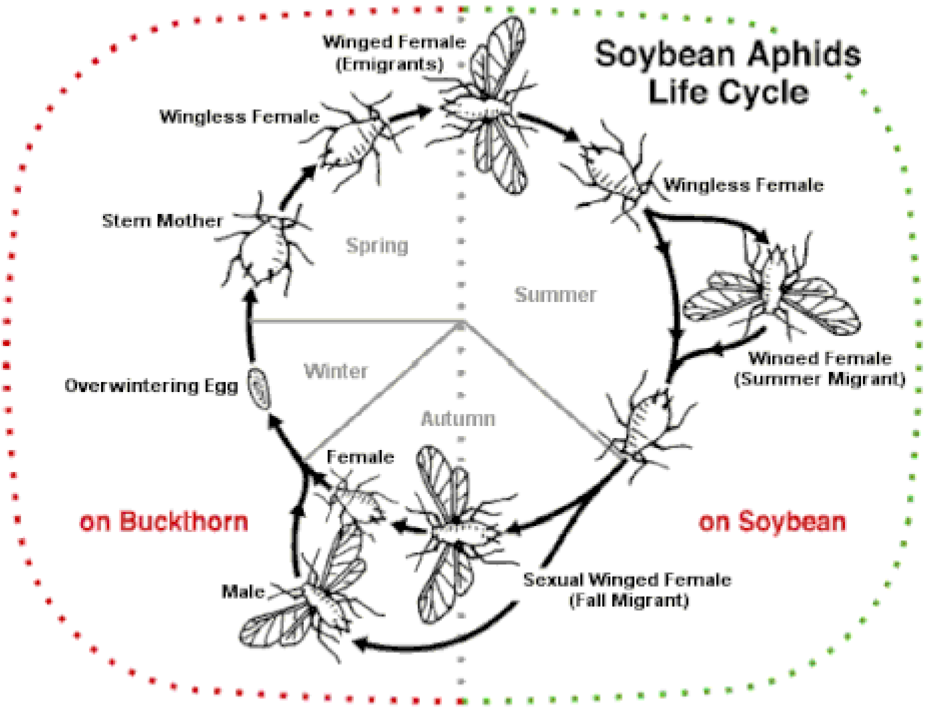
Xylem sap consumption may be related to osmoregulation.[37] High osmotic pressure in the stomach, caused by high sucrose concentration, can lead to water transfer from the hemolymph to the stomach, thus resulting in hyperosmotic stress and eventually to the death of the insect. Aphids avoid this fate by osmoregulating through several processes. Sucrose concentration is directly reduced by assimilating sucrose toward metabolism and by synthesizing oligosaccharides from several sucrose molecules, thus reducing the solute concentration and consequently the osmotic pressure.[39][40] Oligosaccharides are then excreted through honeydew, explaining its high sugar concentrations, which can then be used by other animals such as ants. Furthermore, water is transferred from the hindgut, where osmotic pressure has already been reduced, to the stomach to dilute stomach content.[41] Eventually, aphids consume xylem sap to dilute the stomach osmotic pressure.[37] All these processes function synergetically, and enable aphids to feed on high-sucrose-concentration plant sap, as well as to adapt to varying sucrose concentrations.[37]

Plant sap is an unbalanced diet for aphids, as it lacks essential amino acids, which aphids, like all animals, cannot synthesise, and possesses a high osmotic pressure due to its high sucrose concentration.[34][42] Essential amino acids are provided to aphids by bacterial endosymbionts, harboured in special cells, bacteriocytes.[43] These symbionts recycle glutamate, a metabolic waste of their host, into essential amino acids.[44][45]

Carotenoids and photoheterotrophy

Some species of aphids have acquired the ability to synthesise red carotenoids by horizontal gene transfer from fungi.[46] They are the only animals other than two-spotted spider mites with this capability.[47] Using their carotenoids, aphids may well be able to absorb solar energy and convert it to a form that their cells can use, ATP. This is the only known example of photoheterotrophy in animals. The carotene pigments in aphids form a layer close to the surface of the cuticle, ideally placed to absorb sunlight. The excited carotenoids seem to reduce NAD to NADH which is oxidized in the mitochondria for energy.[48]

Reproduction



Soybean aphid alternates between hosts and between asexual and sexual reproduction.[49]

The simplest reproductive strategy is for an aphid to have a single host all year round. On this it may alternate between sexual and asexual generations (holocyclic) or alternatively, all young may be produced by parthenogenesis, eggs never being laid (anholocyclic). Some species can have both holocyclic and anholocyclic populations under different circumstances but no known aphid species reproduce solely by sexual means.[50] The alternation of sexual and asexual generations may have evolved repeatedly.[51]

However, aphid reproduction is often more complex than this and involves migration between different host plants. In about 10% of species, there is an alternation between woody (primary hosts) on which the aphids overwinter and herbaceous (secondary) host plants, where they reproduce abundantly in the summer.[20][50] A few species can produce a soldier caste, other species show extensive polyphenism under different environmental conditions and some can control the sex ratio of their offspring depending on external factors.[52]

When a typical sophisticated reproductive strategy is used, only females are present in the population at the beginning of the seasonal cycle (although a few species of aphids have been found to have both male and female sexes at this time). The overwintering eggs that hatch in the spring result in females, called fundatrices (stem mothers). Reproduction typically does not involve males (parthenogenesis) and results in live birth (viviparity).[53] The live young are produced by pseudoplacental viviparity, which is the development of eggs, deficient in yolk, the embryos fed by a tissue acting as a placenta. The young emerge from the mother soon after hatching.[54]

Eggs are parthenogenetically produced without meiosis[55][53] and the offspring are clonal to their mother, so they are all female (thelytoky).[11][54] The embryos develop within the mothers' ovarioles, which then give birth to live (already hatched) first-instar female nymphs. As the eggs begin to develop immediately after ovulation, an adult female can house developing female nymphs which already have parthenogenetically developing embryos inside them. This telescoping of generations enables aphids to increase in number with great rapidity. The offspring resemble their parent in every way except size. Thus, a female's diet can affect the body size and birth rate of more than two generations (daughters and granddaughters).[11][56][57]

This process repeats itself throughout the summer, producing multiple generations that typically live 20 to 40 days. For example, some species of cabbage aphids (like *Brevicoryne brassicae*) can produce up to 41 generations of females in a season. Thus, one female hatched in spring can theoretically produce billions of descendants, were they all to survive.[58]

Aphid giving birth to live young: populations are often entirely female.

In autumn, aphids reproduce sexually and lay eggs. Environmental factors such as change in photoperiod and temperature, or perhaps a lower food quantity or quality, causes females to parthenogenetically produce sexual females and males.[55] The males are genetically identical to their mothers except that, with the aphids' X0 sex-determination system, they have one fewer sex chromosome.[55] These sexual aphids may lack wings or even mouthparts.[20] Sexual females and males mate, and females lay eggs that develop outside the mother. The eggs survive the winter and hatch into winged (alate) or wingless females the following spring. This occurs in, for example, the life cycle of the rose aphid (*Macrosiphum rosae*), which may be considered typical of the family. However, in warm environments, such as in the tropics or in a greenhouse, aphids may go on reproducing asexually for many years.[29]

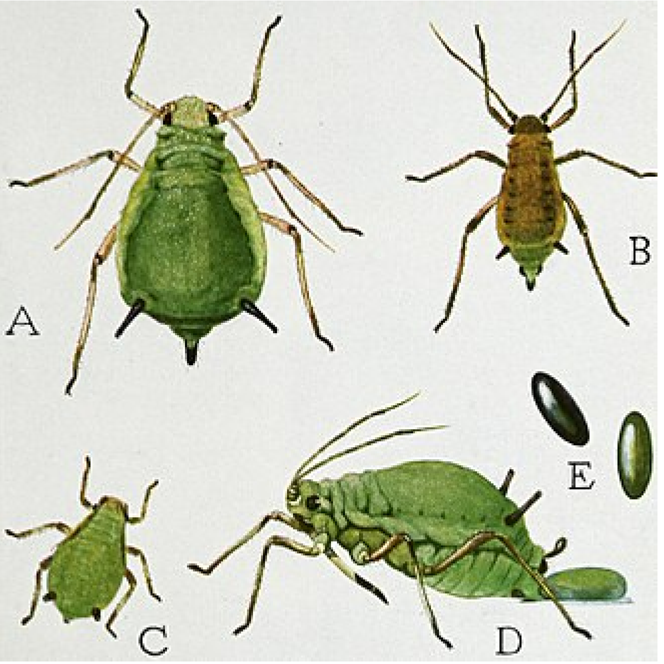
Aphids reproducing asexually by parthenogenesis can have genetically identical winged and non-winged female progeny. Control is complex; some aphids alternate during their life-cycles between genetic control (polymorphism) and environmental control (polyphenism) of production of winged or wingless forms.[59] Winged progeny tend to be produced more abundantly under unfavorable or stressful conditions. Some species produce winged progeny in response to low food quality or quantity. e.g. when a host plant is starting to senesce.[60] The winged females migrate to start new colonies on a new host plant. For example, the apple aphid (*Aphis pomi*), after producing many generations of wingless females gives rise to winged forms that fly to other branches or trees of its typical food plant.[61] Aphids that are attacked by ladybugs, lacewings, parasitoid wasps, or other predators can change the dynamics of their progeny production. When aphids are attacked by these predators, alarm pheromones, in particular beta-farnesene, are released from the cornicles. These alarm pheromones cause several behavioral modifications that, depending on the aphid species, can include walking away and dropping off the host plant. Additionally, alarm pheromone perception can induce the aphids to produce winged progeny that can leave the host plant in search of a safer feeding site.[62] Viral infections, which can be extremely harmful to aphids, can also lead to the production of winged offspring.[63] For example, *Densovirus* infection has a negative impact on rosy apple aphid (*Dysaphis plantaginea (https://influentialpoints.com/Gallery/Dysaphis_plantaginea_Rosy_apple_aphid.htm)*) reproduction, but contributes to the development of aphids with wings, which can transmit the virus more easily to new host plans.[64] Additionally, symbiotic bacteria that live inside of the aphids can also alter aphid reproductive strategies based on the exposure to environmental stressors.[65]

In the autumn, host-alternating (heteroecious) aphid species produce a special winged generation that flies to different host plants for the sexual part of the life cycle. Flightless female and male sexual forms are produced and lay eggs .[66] Some species such as *Aphis fabae* (blackfly of beans), *Metopolophium dirhodum* (rose-grain aphid), *Myzus persicae* (peach-potato aphid), and *Rhopalosiphum padi* (bird cherry-oat aphid) and *Aphis glycines* (soybean aphid)[49] are serious pests. They overwinter on tree or bush primary hosts; in summer, they migrate to their secondary host on a herbaceous plant, often a crop, then the gynoparae return to the tree in autumn. Another example is the soybean aphid (*Aphis glycines*). As fall approaches, the soybean plants begin to senesce from the bottom upwards. The aphids are forced upwards and start to produce winged forms, first females and later males, which fly off to the primary host, buckthorn. Here they mate and overwinter as eggs.[49]

Ecology

Ant mutualism

Some species of ants farm aphids, protecting them on the plants where they are feeding, and consuming the honeydew the aphids release from the terminations of their alimentary canals. This is a mutualistic relationship, with these dairying ants milking the aphids by stroking them with their antennae.[b][67] Although mutualistic, the feeding behaviour of aphids is altered by ant attendance. Aphids attended by ants tend to increase the production of honeydew in smaller drops with a greater concentration of amino acids.[68]



The life stages of the green apple aphid (*Aphis pomi*). Drawing by Robert Evans Snodgrass, 1930

Some farming ant species gather and store the aphid eggs in their nests over the winter. In the spring, the ants carry the newly hatched aphids back to the plants. Some species of dairying ants (such as the European yellow meadow ant, *Lasius flavus*)[69] manage large herds of aphids that feed on roots of plants in the ant colony. Queens leaving to start a new colony take an aphid egg to found a new herd of underground aphids in the new colony. These farming ants protect the aphids by fighting off aphid predators.[67]


Ants tending aphids


An ant guards its aphids


Ant extracting honeydew from an aphid

An interesting variation in ant–aphid relationships involves lycaenid butterflies and *Myrmica* ants. For example, *Niphanda fusca* butterflies lay eggs on plants where ants tend herds of aphids. The eggs hatch as caterpillars which feed on the aphids. The ants do not defend the aphids from the caterpillars, since the caterpillars produce a pheromone which deceives the ants into treating them like ants, and carrying the caterpillars into their nest. Once there, the ants feed the caterpillars, which in return produce honeydew for the ants. When the caterpillars reach full size, they crawl to the colony entrance and form cocoons. After two weeks, the adult butterflies emerge and take flight. At this point, the ants attack the butterflies, but the butterflies have a sticky wool-like substance on their wings that disables the ants' jaws, allowing the butterflies to fly away without being harmed.[70] Some bees in coniferous forests collect aphid honeydew to make forest honey.[29]

Another ant-mimicking gall aphid, *Paracletus cimiciformis* (Eriosomatinae), has evolved a complex double strategy involving two morphs of the same clone and *Tetramorium* ants. Aphids of the round morph cause the ants to farm them, as with many other aphids. The flat morph aphids are aggressive mimics with a "wolf in sheep's clothing" strategy: they have hydrocarbons in their cuticle that mimic those of the ants, and the ants carry them into the brood chamber of the ants' nest and raise them like ant larvae. Once there, the flat morph aphids behave as predators, drinking the body fluids of ant larvae.[71]

Bacterial endosymbiosis

Endosymbiosis with micro-organisms is common in insects, with more than 10% of insect species relying on intracellular bacteria for their development and survival.[72] Aphids harbour a vertically transmitted (from parent to its offspring) obligate symbiosis with *Buchnera aphidicola*, the primary symbiont, inside specialised cells, the bacteriocytes.[73] Five of the bacteria genes have been transferred to the aphid nucleus.[74] The original contamination occurred in a common ancestor 280 to 160 million years ago and enabled aphids to exploit a new ecological niche, feeding on phloem-sap of vascular plants. *B. aphidicola* provides its host with essential amino acids, which are present in low concentrations in plant sap. The stable intracellular conditions, as well as the bottleneck effect experienced during the transmission of a few bacteria from the mother to each nymph, increase the probability of transmission of mutations and gene deletions.[75][76] As a result, the size of the *B. aphidicola* genome is greatly reduced, compared to its putative ancestor.[77] Despite the apparent loss of transcription factors in the reduced genome, gene expression is highly regulated, as shown by the ten-fold variation in expression levels between different genes under normal conditions.[78] *Buchnera aphidicola* gene transcription, although not well understood, is thought to be regulated by a small number of global transcriptional regulators and/or through nutrient supplies from the aphid host.[79]

Some aphid colonies also harbour secondary or facultative (optional extra) bacterial symbionts. These are vertically transmitted, and sometimes also horizontally (from one lineage to another and possibly from one species to another).[80][81] So far, the role of only some of the secondary symbionts has been described; *Regiella insecticola* plays a role in defining the host-plant range,[82][83] *Hamiltonella defensa* provides resistance to parasitoids but only when it is in turn infected by the bacteriophage APSE,[84][85] and *Serratia symbiotica* prevents the deleterious effects of heat.[86]

Predators

Aphids are eaten by many bird and insect predators. In a study on a farm in North Carolina, six species of passerine bird consumed nearly a million aphids per day between them, the top predators being the American goldfinch, with aphids forming 83% of its diet, and the vesper sparrow.[87] Insects that attack aphids include the adults and larvae of predatory ladybirds, hoverfly larvae, parasitic wasps, aphid midge larvae, "aphid lions" (the larvae of green lacewings), and arachnids such as crab spiders. Among ladybirds, *Myzia oblongoguttata* is a dietary specialist which only feeds on conifer aphids, whereas *Adalia bipunctata* and *Coccinella septempunctata* are generalists, feeding on large numbers of species. The eggs are laid in batches, each female laying several hundred. Female hoverflies lay several thousand eggs. The adults feed on pollen and nectar but the larvae feed voraciously on aphids; *Eupeodes corollae* adjusts the number of eggs laid to the size of the aphid colony.[88]

Aphids are often infected by bacteria, viruses, and fungi. They are affected by the weather, such as precipitation,[89] temperature[90] and wind.[91] Fungi that attack aphids include *Neozygites fresenii*, *Entomophthora*, *Beauveria bassiana*, *Metarhizium anisopliae*, and entomopathogenic fungi such as *Lecanicillium lecanii*. Aphids brush against the microscopic spores. These stick to the aphid, germinate, and penetrate the aphid's skin. The fungus grows in the aphid's hemolymph. After about three days, the aphid dies and the fungus releases more spores into the air. Infected aphids are covered with a woolly mass that progressively grows thicker until the aphid is obscured. Often, the visible fungus is not the one that killed the aphid, but a secondary infection.[89]

Aphids can be easily killed by unfavourable weather, such as late spring freezes.[92] Excessive heat kills the symbiotic bacteria that some aphids depend on, which makes the aphids infertile.[93] Rain prevents winged aphids from dispersing, and knocks aphids off plants and thus kills them from the impact or by starvation,[89][94][95] but cannot be relied on for aphid control.[96]

Predators eating aphids

Ladybird larva

Hoverfly larva

The ladybird beetle *Propylea quatuordecimpunctata*

Anti-predator defences

Aphid secreting defensive fluid from the cornicles

Most aphids have little protection from predators. Some species interact with plant tissues forming a gall, an abnormal swelling of plant tissue. Aphids can live inside the gall, which provides protection from predators and the elements. A number of galling aphid species are known to produce specialised "soldier" forms, sterile nymphs with defensive features which defend the gall from invasion.[29][97][98] For example, Alexander's horned aphids are a type of soldier aphid that has a hard exoskeleton and pincer-like mouthparts.[70]:144 A woolly aphid, *Colophina clematis*, has first instar "soldier" larvae that protect the aphid colony, killing larvae of ladybirds, hoverflies and the flower bug *Anthocoris nemoralis* by climbing on them and inserting their stylets.[99]

Although aphids cannot fly for most of their life cycle, they can escape predators and accidental ingestion by herbivores by dropping off the plant onto the ground.[100] Others species use the soil as a permanent protection, feeding on the vascular systems of roots and remaining underground all their lives. They are often attended by ants, for the honeydew they produce, and are carried from plant to plant by the ants through their tunnels.[87]

Some species of aphid, known as "woolly aphids" (Eriosomatinae), excrete a "fluffy wax coating" for protection.[29] The cabbage aphid, *Brevicoryne brassicae*, sequesters secondary metabolites from its host, stores them and releases chemicals that produce a violent chemical reaction and strong mustard oil smell to repel predators.[101] Peptides produced by aphids, Thaumatins, are thought to provide them with resistance to some fungi.[102]

It was common at one time to suggest that the cornicles were the source of the honeydew, and this was even included in the *Shorter Oxford English Dictionary*[103] and the 2008 edition of the *World Book Encyclopedia*.[104] In fact, honeydew secretions are produced from the anus of the aphid,[105] while cornicles mostly produce defensive chemicals such as waxes. There also is evidence of cornicle wax attracting aphid predators in some cases.[106]

Some clones of *Aphis craccivora* are sufficiently toxic to the invasive and dominant predatory ladybird *Harmonia axyridis* to suppress it locally, favouring other ladybird species; the toxicity is in this case narrowly specific to the dominant predator species.[107]

Parasitoids

Aphids are abundant and widespread, and serve as hosts to a large number of parasitoids, many of them being very small (c. 0.1 inches (2.5 mm) long) parasitoid wasps.[108] One species, *Aphis ruborum*, for example, is host to at least 12 species of parasitoid wasps.[109] Parasitoids have been investigated intensively as biological control agents, and many are used commercially for this purpose.[110]

Plant-aphid interactions

Aphids on plant host

Plants mount local and systemic defences against aphid attack. Young leaves in some plants contain chemicals which discourage attack while the older leaves have lost this resistance, while in other plant species, resistance is acquired by older tissues and the young shoots are vulnerable. Volatile products from interplanted onions have been shown to prevent aphid attack on adjacent potato plants by encouraging the production of terpenoids, a benefit exploited in the traditional practice of companion planting, while plants neighbouring infested plants showed increased root growth at the expense of the extension of aerial parts.[31] The wild potato, *Solanum berthaultii*, produces an aphid alarm pheromone, (E)-β-farnesene, as an allomone, a pheromone to ward off attack; it effectively repels the aphid *Myzus persicae* at a range of up to 3 millimetres.[111] *S. berthaultii* and other wild potato species have a further anti-aphid defence in the form of glandular hairs which, when broken by aphids, discharge a sticky liquid that can immobilise some 30% of the aphids infesting a plant.[112]

Plants exhibiting aphid damage can have a variety of symptoms, such as decreased growth rates, mottled leaves, yellowing, stunted growth, curled leaves, browning, wilting, low yields and death. The removal of sap creates a lack of vigour in the plant, and aphid saliva is toxic to plants. Aphids frequently transmit plant viruses to their hosts, such as to potatoes, cereals, sugarbeets, and citrus plants.[29] The green peach aphid, *Myzus persicae*, is a vector for more than 110 plant viruses. Cotton aphids (*Aphis gossypii*) often infect sugarcane, papaya and peanuts with viruses.[20] In plants which produce the phytoestrogen coumestrol, such as alfalfa, damage by aphids is linked with higher concentrations of coumestrol.[113]

The coating of plants with honeydew can contribute to the spread of fungi which can damage plants.[114][115] Honeydew produced by aphids has been observed to reduce the effectiveness of fungicides as well.[116]

Aphid with honeydew, from the anus not the cornicles

A hypothesis that insect feeding may improve plant fitness was floated in the mid-1970s by Owen and Wiegert. It was felt that the excess honeydew would nourish soil micro-organisms, including nitrogen fixers. In a nitrogen poor environment, this could provide an advantage to an infested plant over an uninfested plant. However, this does not appear to be supported by the observational evidence.[117]

Sociality

Some aphids show some of the traits of eusociality, joining insects such as ants, bees and termites. However, there are differences between these sexual social insects and the clonal aphids, which are all descended from a single female parthenogenetically and share an identical genome. About fifty species of aphid, scattered among the closely related, host-alternating families Pemphigidae and Hormaphididae, have some type of defensive morph. These are gall-creating species, with the colony living and feeding inside a gall that they form in the host's tissues. Among the clonal population of these aphids there may be a number of distinct morphs and this lays the foundation for a possible specialisation of function, in this case, a defensive caste. The soldier morphs are mostly first and second instars with the third instar being involved in *Eriosoma moriokense* and only in *Smythurodes betae* are adult soldiers known. The hind legs of soldiers are clawed, heavily sclerotised and the stylets are robust making it possible to rupture and crush small predators.[118] The larval soldiers are altruistic individuals, unable to advance to breeding adults but acting permanently in the interests of the colony. Another requirement for the development of sociality is provided by the gall, a colonial home to be defended by the soldiers.[119]

The soldiers of gall forming aphids also carry out the job of cleaning the gall. The honeydew secreted by the aphids is coated in a powdery wax to form "liquid marbles"[120] that the soldiers roll out of the gall through small orifices.[98] Aphids that form closed galls use the plant's vascular system for their plumbing: the inner surfaces of the galls are highly absorbent and wastes are absorbed and carried away by the plant.[98]

Interactions with humans

Pest status

About 5000 species of aphid have been described and of these, some 450 species have colonised food and fibre crops. As direct feeders on plant sap, they damage crops and reduce yields, but they have a greater impact by being vectors of plant viruses. The transmission of these viruses depends on the movements of aphids between different parts of a plant, between nearby plants and further afield. In this respect, the probing behaviour of an aphid tasting a host is more damaging than lengthy aphid feeding and reproduction by stay-put individuals. The movement of aphids influences the timing of virus epidemics.[121]

Aphids, especially during large outbreaks, have been known to trigger allergic inhalant reactions in sensitive humans.[122]

Dispersal can be by walking or flight, appetitive dispersal or by migration. Winged aphids are weak fliers, lose their wings after a few days and only fly by day. Dispersal by flight is affected by impact, air currents, gravity, precipitation and other factors, or dispersal may be accidental, caused by movement of plant materials, animals, farm machinery, vehicles or aircraft.[121]

Control

Parasitoid braconid wasp ovipositing in black bean aphid

Insecticide control of aphids is difficult, as they breed rapidly, so even small areas missed may enable the population to recover promptly. Aphids may occupy the undersides of leaves where spray misses them, while systemic insecticides do not move satisfactorily into flower petals. Finally, some aphid species are resistant to common insecticide classes including carbamates, organophosphates, and pyrethroids.[123]

For small backyard infestations, spraying plants thoroughly with a strong water jet every few days may be sufficient protection. An insecticidal soap solution can be an effective household remedy to control aphids, but it only kills aphids on contact and has no residual effect. Soap spray may damage plants, especially at higher concentrations or at temperatures above 32 °C (90 °F); some plant species are sensitive to soap sprays.[110][124][125]

Integrated pest management of various species of aphids can be achieved using biological insecticides based on fungi such as *Lecanicillium lecanii*, *Beauveria bassiana* or *Isaria fumosorosea*.[126] Fungi are the main pathogens of aphids; Entomophthorales can quickly cut aphid numbers in nature.[127]

Aphids may also be controlled by the release of natural enemies, in particular lady beetles and parasitoid wasps. However, since adult lady beetles tend to fly away within 48 hours after release, without laying eggs, repeated applications of large numbers of lady beetles are needed to be effective. For example, one large, heavily infested rose bush may take two applications of 1500 beetles each.[110][128]

The ability to produce allomones such as farnesene to repel and disperse aphids and to attract their predators has been experimentally transferred to transgenic *Arabidopsis thaliana* plants using an Eβf synthase gene in the hope that the approach could protect transgenic crops.[129] Eβ farnesene has however found to be ineffective in crop situations although stabler synthetic

forms help improve the effectiveness of control using fungal spores and insecticides through increased uptake caused by movements of aphids.[130]

Green peach aphid, *Myzus persicae*, killed by the fungus *Pandora neoaphidis* (Entomophthorales)

In human culture

Aphids are familiar to farmers and gardeners, mainly as pests. Peter Marren and Richard Mabey record that Gilbert White described an invading "army" of black aphids that arrived in his village of Selborne in August 1774 in "great clouds", covering every plant, while in the unusually hot summer of 1783, White found that honeydew was so abundant as to "deface and destroy the beauties of my garden", though he thought the aphids were consuming rather than producing it.[131]

Infestation of the Chinese sumac (*Rhus chinensis*) by Chinese sumac aphids (*Schlechtendalia chinensis*) can create "Chinese galls" which are valued as a commercial product. As "Galla Chinensis", they are used in traditional Chinese medicine to treat coughs, diarrhoea, night sweats, dysentery and to stop intestinal and uterine bleeding. Chinese galls are also an important source of tannins.[29]

See also

- Aeroplankton
- Economic entomology
- Pineapple gall

Notes

a. The term "black fly" is also used for the Simuliidae, among them the vector of river blindness.

b. Dairying ants also milk mealybugs and other insects.

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Caterpillar

Caterpillars /ˈkætərˌpɪlər/ are the larval stage of members of the order Lepidoptera (the insect order comprising butterflies and moths).

Caterpillar of *Papilio machaon*

As with most common names, the application of the word is arbitrary, since the larvae of sawflies commonly are called caterpillars as well.[1][2] Both lepidopteran and symphytan larvae have eruciform body shapes.

Caterpillars of most species are herbivorous (folivorous), but not all; some (about 1%) are insectivorous, even cannibalistic. Some feed on other animal products; for example, clothes moths feed on wool, and horn moths feed on the hooves and horns of dead ungulates.

A monarch butterfly (*Danaus plexippus*) caterpillar feeding on an unopened seed pod of swamp milkweed

Caterpillars are typically voracious feeders and many of them are among the most serious of agricultural pests. In fact many moth species are best known in their caterpillar stages because of the damage they cause to fruits and other agricultural produce, whereas the moths are obscure and do no direct harm. Conversely, various species of caterpillar are valued as sources of silk, as human or animal food, or for biological control of pest plants.

Contents

Etymology

The origins of the word "caterpillar" date from the early 16th century. They derive from Middle English *catirpel*, *catirpeller*, probably an alteration of Old North French *catepelose*: *cate*, cat (from Latin *cattus*) + *pelose*, hairy (from Latin *pilōsus*).[3]

The inchworm, or looper caterpillars from the family Geometridae are so named because of the way they move, appearing to measure the earth (the word *geometrid* means *earth-measurer* in Greek);[4] the primary reason for this unusual locomotion is the elimination of nearly all the prolegs except the clasper on the terminal segment.

A geometrid caterpillar or inchworm

Description

Crochets on a caterpillar's prolegs

Caterpillars have soft bodies that can grow rapidly between moults. Their size varies between species and instars (moults) from as small as 1 mm up to 14 cm.[5] Some larvae of the order Hymenoptera (ants, bees and wasps) can appear like the caterpillars of the Lepidoptera. Such larvae are mainly seen in the sawfly suborder. However while these larvae superficially resemble caterpillars, they can be distinguished by the presence of prolegs on every abdominal segment, an absence of crochets or hooks on the prolegs (these are present on lepidopteran caterpillars), one pair of prominent ocelli on the head capsule, and an absence of the upside-down Y-shaped suture on the front of the head.[6]

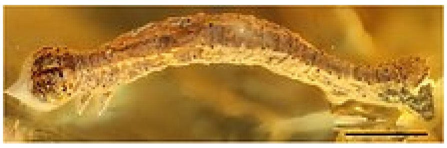
Lepidopteran caterpillars can be differentiated from sawfly larvae by:

- the numbers of pairs of pro-legs; sawfly larvae have 6 or more pairs while caterpillars have a maximum of 5 pairs.
- the number of stemmata (simple eyes); the sawfly larvae have only two,[7] while caterpillars usually have six.
- the presence of crochets on the prolegs; these are absent in the sawflies.
- sawfly larvae have an invariably smooth head capsule with no cleavage lines, while lepidopterous caterpillars bear an inverted "Y" or "V" (adfrontal suture).

Larvae of *Craesus septentrionalis*, a sawfly showing 6 pairs of pro-legs.

Fossils

In 2019, a geometrid moth caterpillar dating back to the Eocene epoch, approximately 44 million years ago, was found preserved in Baltic amber. It was described under *Eogeometer vadens*.[8][9][10] Previously, another fossil dating back approximately 125 million years was found in Lebanese amber.[11][12]



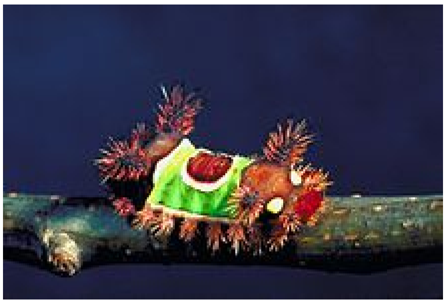
Eogeometer vadens, the earliest known geometrid moth caterpillar found in Baltic amber[8][9][10]

Defenses

Many animals feed on caterpillars as they are rich in protein. As a result, caterpillars have evolved various means of defense.

Caterpillars have evolved defenses against physical conditions such as cold, hot or dry environmental conditions. Some Arctic species like *Gynaephora groenlandica* have special basking and aggregation behaviours[13] apart from physiological adaptations to remain in a dormant state.[14]

Appearance



The saddleback caterpillar has urticating hair and aposematic colouring.

The appearance of a caterpillar can often repel a predator: its markings and certain body parts can make it seem poisonous, or bigger in size and thus threatening, or non-edible. Some types of caterpillars are indeed poisonous or distasteful and their bright coloring is aposematic. Others may mimic dangerous caterpillars or other animals while not being dangerous themselves. Many caterpillars are cryptically colored and resemble the plants on which they feed. An example of caterpillars that use camouflage for defence is the species *Nemoria arizonaria*. If the caterpillars hatch in the spring and feed on oak catkins they appear green. If they hatch in the summer they appear dark colored, like oak twigs. The differential development is linked to the tannin content in the diet.[15] Caterpillars may even have spines or growths that resemble plant parts such as thorns. Some look like objects in the environment such as bird droppings. Some Geometridae cover themselves in plant parts, while bagworms construct and live in a bag covered in sand, pebbles or plant material.

Costa Rican hairy caterpillar. The spiny bristles are a self-defense mechanism

Chemical defenses

More aggressive self-defense measures are taken by some caterpillars. These measures include having spiny bristles or long fine hair-like setae with detachable tips that will irritate by lodging in the skin or mucous membranes.[6] However some birds (such as cuckoos) will swallow even the hairiest of caterpillars. Other caterpillars acquire toxins from their host plants that render them unpalatable to most of their predators. For instance, ornate moth caterpillars utilize pyrrolizidine alkaloids that they obtain from their food plants to deter predators.[16] The most aggressive caterpillar defenses are bristles associated with venom glands. These bristles are called urticating hairs. A venom which is among the most potent defensive chemicals in any animal is produced by the South American silk moth genus *Lonomia*. Its venom is an anticoagulant powerful enough to cause a human to hemorrhage to death (See Lonomiasis).[17] This chemical is being investigated for potential medical applications. Most urticating hairs range in effect from mild irritation to dermatitis. Example: Brown-tail moth.

Giant swallowtail caterpillar everting its osmeterium in defense

Plants contain toxins which protect them from herbivores, but some caterpillars have evolved countermeasures which enable them to eat the leaves of such toxic plants. In addition to being unaffected by the poison, the caterpillars sequester it in their body, making them highly toxic to predators. The chemicals are also carried on into the adult stages. These toxic species, such as the cinnabar moth (*Tyria jacobaeae*) and monarch (*Danaus plexippus*) caterpillars, usually advertise themselves with the danger colors of red, yellow and black, often in bright stripes (see aposematism). Any predator that attempts to eat a caterpillar with an aggressive defense mechanism will learn and avoid future attempts.

Some caterpillars regurgitate acidic digestive juices at attacking enemies. Many papilionid larvae produce bad smells from extrudable glands called osmeteria.

Defensive behaviors

Many caterpillars display feeding behaviors which allow the caterpillar to remain hidden from potential predators. Many feed in protected environments, such as enclosed inside silk galleries, rolled leaves or by mining between the leaf surfaces.

Caterpillars linked together into a "train"

Some caterpillars, like early instars of the tomato hornworm and tobacco hornworm, have long "whip-like" organs attached to the ends of their body. The caterpillar wiggles these organs to frighten away flies and predatory wasps.[18] Some caterpillars can evade predators by using a silk line and dropping off from branches when disturbed. Many species thrash about violently when disturbed to scare away potential predators. One species (*Amorpha juglandis*) even makes high pitched whistles that can scare away birds.[19]

Social behaviors and relationships with other insects

Some caterpillars obtain protection by associating themselves with ants. The Lycaenid butterflies are particularly well known for this. They communicate with their ant protectors by vibrations as well as chemical means and typically provide food rewards.[20]

Some caterpillars are gregarious; large aggregations are believed to help in reducing the levels of parasitization and predation.[21] Clusters amplify the signal of aposematic coloration, and individuals may participate in group regurgitation or displays. Pine processionary (*Thaumetopoea pityocampa*) caterpillars often link into a long train to move through trees and over the ground. The head of the lead caterpillar is visible, but the other heads can appear hidden.[22] Forest tent caterpillars cluster during periods of cold weather.

Predators

Caterpillars suffer predation from many animals. The European pied flycatcher is one species that preys upon caterpillars. The flycatcher typically finds caterpillars among oak foliage. Paper wasps, including those in the genus *Polistes* and *Polybia* catch caterpillars to feed their young and themselves.

Behavior

Caterpillars have been called "eating machines", and eat leaves voraciously. Most species shed their skin four or five times as their bodies grow, and they eventually enter a pupal stage before becoming adults.[23] Caterpillars grow very quickly; for instance, a tobacco hornworm will increase its weight ten-thousandfold in less than twenty days. An adaptation that enables them to eat so much is a mechanism in a specialized midgut that quickly transports ions to the lumen (midgut cavity), to keep the potassium level higher in the midgut cavity than in the hemolymph.[24]

A pasture day moth caterpillar feeding on capeweed

Most caterpillars are solely herbivorous. Many are restricted to feeding on one species of plant, while others are polyphagous. Some, including the clothes moth, feed on detritus. Some are predatory, and may prey on other species of caterpillars (e.g. Hawaiian *Eupithecia*). Others feed on eggs of other insects, aphids, scale insects, or ant larvae. A few are parasitic on cicadas or leaf hoppers (Epipyropidae).[25] Some Hawaiian caterpillars (*Hyposmocoma molluscivora*) use silk traps to capture snails.[26]

A gypsy moth caterpillar

Many caterpillars are nocturnal. For example, the "cutworms" (of the family Noctuidae) hide at the base of plants during the day and only feed at night.[27] Others, such as gypsy moth (Lymantria dispar) larvae, change their activity patterns depending on density and larval stage, with more diurnal feeding in early instars and high densities.[28]

Economic effects

Hypsipyla grandela damages mahogany in Brazil

Caterpillars cause much damage, mainly by eating leaves. The propensity for damage is enhanced by monocultural farming practices, especially where the caterpillar is specifically adapted to the host plant under cultivation. The cotton bollworm causes enormous losses. Other species eat food crops. Caterpillars have been the target of pest control through the use of pesticides, biological control and agronomic practices. Many species have become resistant to pesticides. Bacterial toxins such as those from *Bacillus thuringiensis* which are evolved to affect the gut of Lepidoptera have been used in sprays of bacterial spores, toxin extracts and also by incorporating genes to produce them within the host plants. These approaches are defeated over time by the evolution of resistance mechanisms in the insects.[29]

Plants evolve mechanisms of resistance to being eaten by caterpillars, including the evolution of chemical toxins and physical barriers such as hairs. Incorporating host plant resistance (HPR) through plant breeding is another approach used in reducing the impact of caterpillars on crop plants.[30]

Some caterpillars are used in industry. The silk industry is based on the silkworm caterpillar.

Human health

Buck moth caterpillar sting on a shin twenty-four hours after occurrence in south Louisiana. The reddish mark covers an area about 20 mm at its widest point by about 70 mm in length.

Caterpillar hair can be a cause of human health problems. Caterpillar hairs sometimes have venoms in them and species from approximately 12 families of moths or butterflies worldwide can inflict serious human injuries ranging from urticarial dermatitis and atopic asthma to osteochondritis, consumption coagulopathy, renal failure, and intracerebral hemorrhage.[31] Skin rashes are the most common, but there have been fatalities.[32] *Lonomia* is a frequent cause of envenomation in Brazil, with 354 cases reported between 1989 and 2005. Lethality ranging up to 20% with death caused most often by intracranial hemorrhage.[33]

Caterpillar hair has also been known to cause kerato-conjunctivitis. The sharp barbs on the end of caterpillar hairs can get lodged in soft tissues and mucous membranes such as the eyes. Once they enter such tissues, they can be difficult to extract, often exacerbating the problem as they migrate across the membrane.[34]

This becomes a particular problem in an indoor setting. The hair easily enter buildings through ventilation systems and accumulate in indoor environments because of their small size, which makes it difficult for them to be vented out. This accumulation increases the risk of human contact in indoor environments.[35]

Caterpillars are a food source in some cultures. For example, in South Africa mopane worms are eaten by the bushmen, and in China silkworms are considered a delicacy.

In popular culture

William Blake's illustration of a caterpillar overlooking a child from his illustrated book *For Children The Gates of Paradise*.[36]

In the Old Testament of the Bible caterpillars are feared as pest that devour crops. They are part of the "pestilence, blasting, mildew, locus" because of their association with the locust, thus they are one of the plagues of Egypt. Jeremiah names them as one of the inhabitants of Babylon. The English word caterpillar derives from the old French *catepelose* (hairy cat) but merged with the *piller* (pillager). Caterpillars became a symbol for social dependents. Shakespeare's Bolingbroke described King Richard's friends as "The caterpillars of the commonwealth, Which I have sworn to weed and pluck away". In 1790 William Blake referenced this popular image in The Marriage of Heaven and Hell when he attacked priests: "as the caterpillar chooses the fairest leaves to lay her eggs on, so the priest lay his curse on the fairest joys".[37]

The role of caterpillars in the life stages of butterflies was badly understood. In 1679 Maria Sibylla Merian published the first volume of *The Caterpillars' Marvelous Transformation and Strange Floral Food*, which contained 50 illustrations and a description of insects, moths, butterflies and their larvae.[38] An earlier popular publication on moths and butterflies, and their caterpillars, by Jan Goedart had not included eggs in the life stages of European moths and butterflies, because he had believed that caterpillars were generated from water. When Merian published her study of caterpillars it was still widely believed that insects were spontaneously generated. Merian's illustrations supported the findings of Francesco Redi, Marcello Malpighi and Jan Swammerdam.[39]

A 1907 illustrations by Arthur Rackham of the Caterpillar talking to Alice in Alice's Adventures in Wonderland

Butterflies were regarded as symbol for the human soul since ancient time, and also in the Christian tradition.[40] Goedart thus located his empirical observations on the transformation of caterpillars into butterflies in the Christian tradition. As such he argued that the metamorphosis from caterpillar into butterfly was a symbol, and even proof, of Christ's resurrection. He argued "that from dead caterpillars emerge living animals; so it is equally true and miraculous, that our dead and rotten corpses will rise from the grave."[41] Swammerdam, who in 1669 had demonstrated that inside a caterpillar the rudiments of the future butterfly's limbs and wings could be discerned, attacked the mystical and religious notion that the caterpillar died and the butterfly subsequently resurrected.[42] As a militant Cartesian, Swammerdam attacked Goedart as ridiculous, and when publishing his findings he proclaimed "here we witness the digression of those who have tried to prove Resurrection of the Dead from these obviously natural and comprehensible changes within the creature itself."[43]

Since then the metamorphoses of the caterpillar into a butterfly has in Western societies been associated with countless human transformations in folktales and literature. There is no process in the physical life of human beings that resembles this metamorphoses, and the symbol of the caterpillar tends to depict a psychic transformation of a human. As such the caterpillar has in the Christian tradition become a metaphor for being "born again".[44]

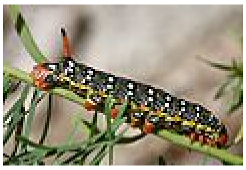
Famously, in Lewis Carroll's Alice's Adventures in Wonderland a caterpillar asks Alice "Who are you?". When Alice comments on the caterpillar's inevitable transformation into a butterfly, the caterpillar champions the position that in spite of changes it is still possible to know something, and that Alice is the same Alice at the beginning and end of a considerable interval.[45] When the Caterpillar asks Alice to clarify a point, the child replies "I'm afraid I can't put it more clearly... for I can't but understand it

myself, to begin with, and being so many different sizes in a day is very confusing". Here Carroll satirizes René Descartes, the founder of Cartesian philosophy, and his theory on innate ideas. Descartes argued that we are distracted by urgent bodily stimuli that swamp the human mind in childhood. Descartes also theorised that inherited preconceived opinions obstruct the human perception of the truth.[46]

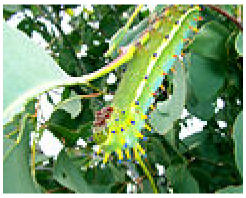
More recent symbolic references to caterpillars in popular media include the *Mad Men* season 3 episode "The Fog", in which Betty Draper has a drug-induced dream, while in labor, that she captures a caterpillar and holds it firmly in her hand.[47] In *The Sopranos* season 5 episode "The Test Dream", Tony Soprano dreams that Ralph Cifaretto has a caterpillar on his bald head that changes into a butterfly.

Gallery

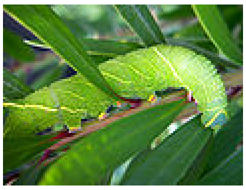
Click left or right for a slide show.



Caterpillar of the spurge hawk-moth, near Binn, Valais, Switzerland at c. 2 km altitude.



Caterpillar of the emperor gum moth.

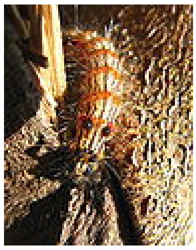


A poplar hawk-moth caterpillar (a common species of caterpillar in the UK).

Ant tending a lycaenid caterpillar.

Life cycle of the red-humped caterpillar (*Schizura concinna*).

Forest tent caterpillar (Malacosoma disstria)



Camouflage: apparently with eight eyes, only two of them are real. Photo in a eucalyptus tree, São Paulo, Brazil

Caterpillar of the Polyphemus moth (*Antheraea polyphemus*), Virginia, United States

Caterpillars on an apple tree in Victoria, British Columbia, Canada

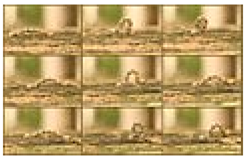
Caterpillar on a leaf

Caterpillar of Belize

Dryas iulia

Caterpillar of great orange tip resembling the common green vine snake (*Ahaetulla nasuta*)

Prepupa of cabbage looper in its cocoon



Locomotion of a small Geometrid caterpillar.

See also

- Edible caterpillars
- Larval food plants of Lepidoptera
- Lepidopterism - caterpillar dermatitis
- List of pests and diseases of roses
- Sericulture

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WIKIPEDIA

Grasshopper

Grasshoppers are a group of insects belonging to the suborder Caelifera. They are among what is probably the most ancient living group of chewing herbivorous insects, dating back to the early Triassic around 250 million years ago.

Grasshoppers are typically ground-dwelling insects with powerful hind legs which allow them to escape from threats by leaping vigorously. As hemimetabolous insects, they do not undergo complete metamorphosis; they hatch from an egg into a nymph or "hopper" which undergoes five moults, becoming more similar to the adult insect at each developmental stage. At high population densities and under certain environmental conditions, some grasshopper species can change color and behavior and form swarms. Under these circumstances, they are known as locusts.

Grasshoppers are plant-eaters, with a few species at times becoming serious pests of cereals, vegetables and pasture, especially when they swarm in their millions as locusts and destroy crops over wide areas. They protect themselves from predators by camouflage; when detected, many species attempt to startle the predator with a brilliantly-coloured wing-flash while jumping and (if adult) launching themselves into the air, usually flying for only a short distance. Other species such as the rainbow grasshopper have warning coloration which deters predators. Grasshoppers are affected by parasites and various diseases, and many predatory creatures feed on both nymphs and adults. The eggs are subject to attack by parasitoids and predators.

Grasshoppers have had a long relationship with humans. Swarms of locusts can have devastating effects and cause famine, and even in smaller numbers, the insects can be serious pests. They are used as food in countries such as Mexico and Indonesia. They feature in art, symbolism and literature.

Grasshopper

Temporal range: 252 Ma–Recent

American grasshopper (*Schistocerca americana*)

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Orthoptera
Suborder:	Caelifera
Infraorder:	Acrididea
Informal group:	Acridomorpha Dirsh, 1966

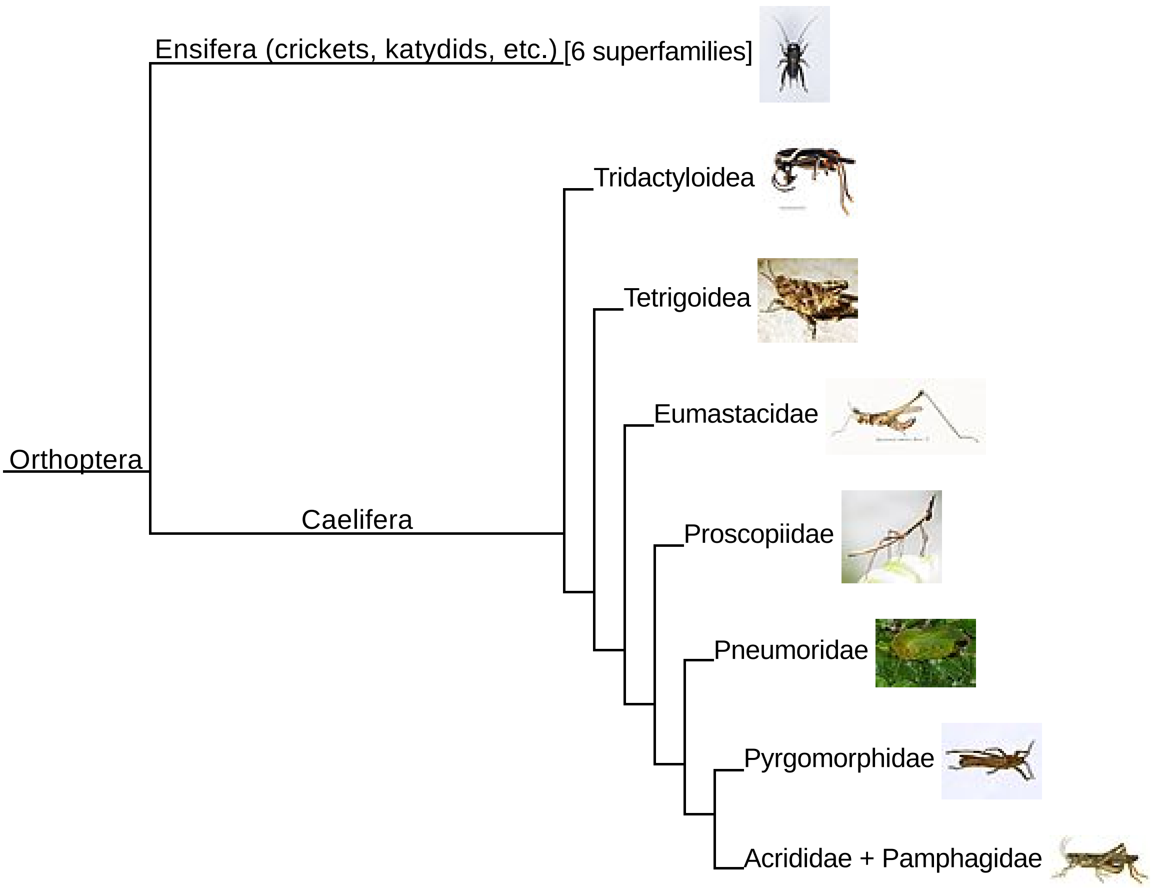
Superfamilies

- Acridoidea
- Eumastacoidea
- Pneumoroidea
- Proscopioidea
- Pyrgomorphoidea
- Tanaoceroidea
- Trigonopterygoidea

Contents

Phylogeny

Grasshoppers belong to the suborder Caelifera. Although, "grasshopper" is sometimes used as a common name for the suborder in general,[1][2][3] some sources restrict it to the more "advanced" groups.[4] They may be placed in the infraorder Acrididea[5] and have been referred-to as "short-horned grasshoppers" in older texts[6] to distinguish them from the also-obsolete term "long-horned grasshoppers" (now bush-crickets or katydids) with their much longer antennae. The phylogeny of the Caelifera, based on mitochondrial ribosomal RNA of thirty-two taxa in six out of seven superfamilies, is shown as a cladogram. The Ensifera (crickets, *etc.*), Caelifera and all the superfamilies of grasshoppers except Pamphagoidea appear to be monophyletic.[7][8]



In evolutionary terms, the split between the Caelifera and the Ensifera is no more recent than the Permo-Triassic boundary;[9] the earliest insects that are certainly Caeliferans are in the extinct families Locustopseidae and Locustavidae from the early Triassic, roughly 250 million years ago. The group diversified during the Triassic and have remained important plant-eaters from that time to now. The first modern families such as the Eumastacidae, Tetrigidae and Tridactylidae appeared in the Cretaceous, though some insects that might belong to the last two of these groups are found in the early Jurassic.[10][11] Morphological classification is difficult because many taxa have converged towards a common habitat type; recent taxonomists have concentrated on the internal genitalia, especially those of the male. This information is not available from fossil specimens, and the palaentological taxonomy is founded principally on the venation of the hindwings.[12]

Fossil grasshoppers at the Royal Ontario Museum

The Caelifera includes some 2,400 valid genera and about 11,000 known species. Many undescribed species probably exist, especially in tropical wet forests. The Caelifera have a predominantly tropical distribution with fewer species known from temperate zones, but most of the superfamilies have representatives worldwide. They are almost exclusively herbivorous and are probably the oldest living group of chewing herbivorous insects.[12]

The most diverse superfamily is the Acridoidea, with around 8,000 species. The two main families in this are the Acrididae (grasshoppers and locusts) with a worldwide distribution, and the Romaleidae (lubber grasshoppers), found chiefly in the New World. The Ommexechidae and Tristiridae are South American, and the Lentulidae, Lithidiidae and Pamphagidae are mainly African. The Pauliniids are nocturnal and can swim or skate on water, and the Lentulids are wingless.[10] Pneumoridae are native to Africa, particularly southern Africa, and are distinguished by the inflated abdomens of the males.[13]

Characteristics

Grasshoppers have the typical insect body plan of head, thorax and abdomen. The head is held vertically at an angle to the body, with the mouth at the bottom. The head bears a large pair of compound eyes which give all-round vision, three simple eyes which can detect light and dark, and a pair of thread-like antennae that are sensitive to touch and smell. The downward-directed mouthparts are modified for chewing and there are two sensory palps in front of the jaws.[14]

The thorax and abdomen are segmented and have a rigid cuticle made up of overlapping plates composed of chitin. The three fused thoracic segments bear three pairs of legs and two pairs of wings. The forewings, known as tegmina, are narrow and leathery while the hindwings are large and membranous, the veins providing strength. The legs are terminated by claws for gripping. The hind leg is particularly powerful; the femur is robust and has several ridges where different surfaces join and the inner ridges bear stridulatory pegs in some species. The posterior edge of the tibia bears a double row of spines and there are a pair of articulated spurs near its lower end. The interior of the thorax houses the muscles that control the wings and legs.[14]

The abdomen has eleven segments, the first of which is fused to the thorax and contains the tympanal organ and hearing system. Segments two to eight are ring-shaped and joined by flexible membranes. Segments nine to eleven are reduced in size; segment nine bears a pair of cerci and segments ten and eleven house the reproductive organs. Female grasshoppers are normally larger than males, with short ovipositors.[14] The name of the suborder "Caelifera" comes from the Latin and means *chisel-bearing*, referring to the shape of the ovipositor.[15]

Those species that make easily heard noises usually do so by rubbing a row of pegs on the hind legs against the edges of the forewings (stridulation). These sounds are produced mainly by males to attract females, though in some species the females also stridulate.[16]

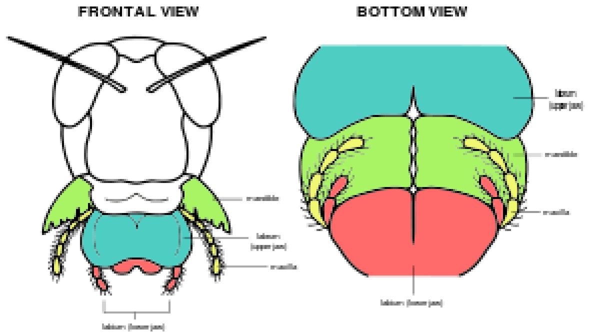
Grasshoppers may be confused with crickets, but they differ in many aspects; these include the number of segments in their antennae and the structure of the ovipositor, as well as the location of the tympanal organ and the methods by which sound is produced.[17] Ensiferans have antennae that can be much longer than the body and have at least 20–24 segments, while caeliferans have fewer segments in their shorter, stouter antennae.[16]

Ensifera, like this great green bush-cricket *Tettigonia viridissima*, somewhat resemble grasshoppers but have over 20 segments in their antennae and different ovipositors.

Biology

Diet and digestion

Most grasshoppers are polyphagous, eating vegetation from multiple plant sources,[18] but some are omnivorous and also eat animal tissue and animal faeces. In general their preference is for grasses, including many cereals grown as crops.[19] The digestive system is typical of insects, with Malpighian tubules discharging into the midgut. Carbohydrates are digested mainly in the crop, while proteins are digested in the ceca of the midgut. Saliva is abundant but largely free of enzymes, helping to move food and Malpighian secretions along the gut. Some grasshoppers possess cellulase, which by softening plant cell walls makes plant cell contents accessible to other digestive enzymes.[20]



Structure of mouthparts

Sensory organs

Grasshoppers have a typical insect nervous system, and have an extensive set of external sense organs. On the side of the head are a pair of large compound eyes which give a broad field of vision and can detect movement, shape, colour and distance. There are also three simple eyes (ocelli) on the forehead which can detect light intensity, a pair of antennae containing olfactory (smell) and touch receptors, and mouthparts containing gustatory (taste) receptors.[21] At the front end of the abdomen there is a pair of tympanal organs for sound reception. There are numerous fine hairs (setae) covering the whole body that act as mechanoreceptors (touch and wind sensors), and these are most dense on the antennae, the palps (part of the mouth), and on the cerci at the tip of the abdomen.[22] There are special receptors (campaniform sensillae) embedded in the cuticle of the legs that sense pressure and cuticle distortion.[23] There are internal "chordotonal" sense organs specialized to detect position and movement about the joints of the exoskeleton. The receptors convey information to the central nervous system through sensory neurons, and most of these have their cell bodies located in the periphery near the receptor site itself.[22]

Frontal view of Egyptian locust (*Anacridium aegyptium*) showing the compound eyes, tiny ocelli and numerous setae

Circulation and respiration

Like other insects, grasshoppers have an open circulatory system and their body cavities are filled with haemolymph. A heart-like structure in the upper part of the abdomen pumps the fluid to the head from where it percolates past the tissues and organs on its way back to the abdomen. This system circulates nutrients throughout the body and carries metabolic wastes to be excreted into

the gut. Other functions of the haemolymph include wound healing, heat transfer and the provision of hydrostatic pressure, but the circulatory system is not involved in gaseous exchange.[24] Respiration is performed using tracheae, air-filled tubes, which open at the surfaces of the thorax and abdomen through pairs of valved spiracles. Larger insects may need to actively ventilate their bodies by opening some spiracles while others remain closed, using abdominal muscles to expand and contract the body and pump air through the system.[25]

Jumping

A large grasshopper, such as a locust, can jump about a metre (twenty body lengths) without using its wings; the acceleration peaks at about 20 g.[26] Grasshoppers jump by extending their large back legs and pushing against the substrate (the ground, a twig, a blade of grass or whatever else they are standing on); the reaction force propels them into the air.[27] They jump for several reasons; to escape from a predator, to launch themselves into flight, or simply to move from place to place. For the escape jump in particular there is strong selective pressure to maximize take-off velocity, since this determines the range. This means that the legs must thrust against the ground with both high force and a high velocity of movement. A fundamental property of muscle is that it cannot contract with high force and high velocity at the same time. Grasshoppers overcome this by using a catapult mechanism to amplify the mechanical power produced by their muscles.[28]

The jump is a three-stage process.[29] First, the grasshopper fully flexes the lower part of the leg (tibia) against the upper part (femur) by activating the flexor tibiae muscle (the back legs of the grasshopper in the top photograph are in this preparatory position). Second, there is a period of co-contraction in which force builds up in the large, pennate extensor tibiae muscle, but the tibia is kept flexed by the simultaneous contraction of the flexor tibiae muscle. The extensor muscle is much stronger than the flexor muscle, but the latter is aided by specialisations in the joint that give it a large effective mechanical advantage over the former when the tibia is fully flexed.[30] Co-contraction can last for up to half a second, and during this period the extensor muscle shortens and stores elastic strain energy by distorting stiff cuticular structures in the leg.[31] The extensor muscle contraction is quite slow (almost isometric), which allows it to develop high force (up to 14 N in the desert locust), but because it is slow only low power is needed. The third stage of the jump is the trigger relaxation of the flexor muscle, which releases the tibia from the flexed position. The subsequent rapid tibial extension is driven mainly by the relaxation of the elastic structures, rather than by further shortening of the extensor muscle. In this way the stiff cuticle acts like the elastic of a catapult, or the bow of a bow-and-arrow. Energy is put into the store at low power by slow but strong muscle contraction, and retrieved from the store at high power by rapid relaxation of the mechanical elastic structures.[32][33]

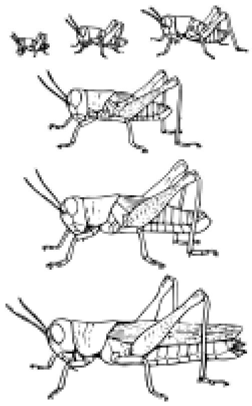
Stridulation

Male grasshoppers spend much of the day stridulating, singing more actively under optimal conditions and being more subdued when conditions are adverse; females also stridulate, but their efforts are insignificant when compared to the males. Late-stage male nymphs can sometimes be seen making stridulatory movements, although they lack the equipment to make sounds, demonstrating the importance of this behavioural trait. The songs are a means of communication; the male stridulation seems to express reproductive maturity, the desire for social cohesion and individual well-being. Social cohesion becomes necessary among grasshoppers because of their ability to jump or fly large distances, and the song can serve to limit dispersal and guide others to favourable habitat. The generalised song can vary in phraseology and intensity, and is modified in the presence of a rival male, and changes again to a courtship song when a female is nearby.[34] In male grasshoppers of the family Pneumoridae, the enlarged abdomen amplifies stridulation.[13]

Life cycle

In most grasshopper species, conflicts between males over females rarely escalate beyond ritualistic displays. Some exceptions include the chameleon grasshopper (*Kosciuscola tristis*), where males may fight on top of ovipositing females; engaging in leg grappling, biting, kicking and mounting.[35]

Romalea microptera grasshoppers: female (larger) is laying eggs, with male in attendance.



Six stages (instars) of development, from newly hatched nymph to fully winged adult

The newly emerged female grasshopper has a preoviposition period of a week or two while she increases in weight and her eggs mature. After mating, the female of most species digs a hole with her ovipositor and lays a batch of eggs in a pod in the ground near food plants, generally in the summer. After laying the eggs, she covers the hole with soil and litter.[14] Some, like the semi-aquatic *Cornops aquaticum*, deposit the pod directly into plant tissue.[36] The eggs in the pod are glued together with a froth in some species. After a few weeks of development, the eggs of most species in temperate climates go into diapause, and pass the winter in this state. Diapause is broken by a sufficiently low ground temperature, with development resuming as soon as the ground warms above a certain threshold temperature. The embryos in a pod generally all hatch out within a few minutes of each other. They soon shed their membranes and their exoskeletons harden. These first instar nymphs can then jump away from predators.[37]

Grasshoppers undergo incomplete metamorphosis: they repeatedly moult, each instar becoming larger and more like an adult, with the wing-buds increasing in size at each stage. The number of instars varies between species but is often six. After the final moult, the wings are inflated and become fully functional. The migratory grasshopper, *Melanoplus sanguinipes*, spends about 25 to 30 days as a nymph, depending on sex and temperature, and lives for about 51 days as an adult.[37]

Swarming

Millions of plague locusts on the move in Australia

Locusts are the swarming phase of certain species of short-horned grasshoppers in the family Acrididae. Swarming behaviour is a response to overcrowding. Increased tactile stimulation of the hind legs causes an increase in levels of serotonin.[38] This causes the grasshopper to change colour, feed more and breed faster. The transformation of a solitary individual into a swarming one is induced by several contacts per minute over a short period.[39]

Following this transformation, under suitable conditions dense nomadic bands of flightless nymphs known as "hoppers" can occur, producing pheromones which attract the insects to each other. With several generations in a year, the locust population can build up from localised groups into vast accumulations of flying insects known as plagues, devouring all the vegetation they encounter. The largest recorded locust swarm was one formed by the now-extinct Rocky Mountain locust in 1875; the swarm was 1,800 miles (2,900 km) long and 110 miles (180 km) wide,[40] and one estimate puts the number of locusts involved at 3.5 trillion.[41] An adult desert locust can eat about 2 g (0.1 oz) of plant material each day, so the billions of insects in a large swarm can be very destructive, stripping all the foliage from plants in an affected area and consuming stems, flowers, fruits, seeds and bark.[42]

Predators, parasites and pathogens

Grasshoppers have a wide range of predators at different stages of their lives; eggs are eaten by bee-flies, ground beetles and blister beetles; hoppers and adults are taken by other insects such as ants, robber flies and sphecid wasps, by spiders, and by many birds and small mammals including dogs and cats.[43]


Cottontop tamarin monkey eating a grasshopper

The eggs and nymphs are under attack by parasitoids including blow flies, flesh flies, and tachinid flies. External parasites of adults and nymphs include mites.[43] Female grasshoppers parasitised by mites produce fewer eggs and thus have fewer offspring than unaffected individuals.[44]


Grasshopper with parasitic mites

The grasshopper nematode (*Mermis nigrescens*) is a long slender worm that infects grasshoppers, living in the insect's hemocoel. Adult worms lay eggs on plants and the host becomes infected when the foliage is eaten.[45] *Spinochordodes tellinii* and *Paragordius tricuspidatus* are parasitic worms that infect grasshoppers and alter the behaviour of their hosts. When the worms are sufficiently developed, the grasshopper is persuaded to leap into a nearby body of water where it drowns, thus enabling the parasite to continue with the next stage of its life cycle, which takes place in water.[46][47]


Locusts killed by the naturally occurring fungus *Metarhizium*, an environmentally friendly means of biological control. CSIRO, 2005[48]

Grasshoppers are affected by diseases caused by bacteria, viruses, fungi and protozoa. The bacteria *Serratia marcescens* and *Pseudomonas aeruginosa* have both been implicated in causing disease in grasshoppers, as has the entomopathogenic fungus *Beauveria bassiana*. This widespread fungus has been used to control various pest insects around the world, but although it infects grasshoppers, the infection is not usually lethal because basking in the sun has the result of raising the insect's temperature above a threshold tolerated by the fungus.[49] The fungal pathogen *Entomophaga grylli* is able to influence the behaviour of its grasshopper host, causing it to climb to the top of a plant and cling to the stem as it dies. This ensures wide dispersal of the fungal spores liberated from the corpse.[50]

The fungal pathogen *Metarhizium acridum* is found in Africa, Australia and Brazil where it has caused epizootics in grasshoppers. It is being investigated for possible use as a microbial insecticide for locust control.[49] The microsporidian fungus *Nosema locustae*, once considered to be a protozoan, can be lethal to grasshoppers. It has to be consumed by mouth and is the basis for a bait-based commercial microbial pesticide. Various other microsporidians and protozoans are found in the gut.[49]

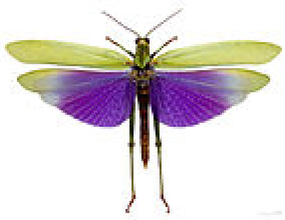
Anti-predator defences

Grasshoppers exemplify a range of anti-predator adaptations, enabling them to avoid detection, to escape if detected, and in some cases to avoid being eaten if captured. Grasshoppers are often camouflaged to avoid detection by predators that hunt by sight; some species can change their coloration to suit their surroundings.[51]

Several species such as the hooded leaf grasshopper *Phyllochoreia ramakrishnai* (Eumastacoidea) are detailed mimics of leaves. Stick grasshoppers (Proscopiidae) mimic wooden sticks in form and coloration.[52] Grasshoppers often have deimatic patterns on their wings, giving a sudden flash of bright colours that may startle predators long enough to give time to escape in a combination of jump and flight.[53]

Some species are genuinely aposematic, having both bright warning coloration and sufficient toxicity to dissuade predators. *Dictyophorus productus* (Pyrgomorphidae) is a "heavy, bloated, sluggish insect" that makes no attempt to hide; it has a bright red abdomen. A *Cercopithecus* monkey that ate other grasshoppers refused to eat the species.[54] Another species, the rainbow or painted grasshopper of Arizona, *Dactylotum bicolor* (Acridoidea), has been shown by experiment with a natural predator, the little striped whiptail lizard, to be aposematic.[55]

Gaudy grasshopper, *Atractomorpha lata*, evades predators with camouflage.



Lubber grasshopper, *Titanacris albipes*, has deimatically coloured wings, used to startle predators.

Leaf grasshopper, *Phyllochoreia ramakrishnai*, mimics a green leaf.

Painted grasshopper, *Dactylotum bicolor*, deters predators with warning coloration.

Spotted grasshopper, *Aularches miliaris*, defends itself with toxic foam and warning colours.[56]

Relationship with humans

In art and media

Detail of grasshopper on table in Rachel Ruysch's painting *Flowers in a Vase*, c. 1685. National Gallery, London

Grasshoppers are occasionally depicted in artworks, such as the Dutch Golden Age painter Balthasar van der Ast's still life oil painting, *Flowers in a Vase with Shells and Insects*, c. 1630, now in the National Gallery, London, though the insect may be a bush-cricket.[57]

Another orthopteran is found in Rachel Ruysch's still life *Flowers in a Vase*, c. 1685. The seemingly static scene is animated by a "grasshopper on the table that looks about ready to spring", according to the gallery curator Betsy Wieseman, with other invertebrates including a spider, an ant, and two caterpillars.[58][59]

Grasshoppers are also featured in cinema. The 1957 film *Beginning of the End* portrayed giant grasshoppers attacking Chicago.[60] In the 1998 Disney/Pixar animated film *A Bug's Life*, the heroes are Flik and the ant colony, and Hopper and his henchmen are the grasshoppers.[61]

Symbolism

Sir Thomas Gresham's gilded grasshopper symbol, Lombard Street, London, 1563

Grasshoppers are sometimes used as symbols.[62] During the Greek Archaic Era, the grasshopper was the symbol of the *polis* of Athens,[63] possibly because they were among the most common insects on the dry plains of Attica.[63] Native Athenians for a while wore golden grasshopper brooches to symbolise that they were of pure Athenian lineage with no foreign ancestors.[63] Another symbolic use of the grasshopper is Sir Thomas Gresham's gilded grasshopper in Lombard Street, London, dating from 1563;[a] the building was for a while the headquarters of the Guardian Royal Exchange, but the company declined to use the symbol for fear of confusion with the locust.[64]

When grasshoppers appear in dreams, these have been interpreted as symbols of "Freedom, independence, spiritual enlightenment, inability to settle down or commit to decision". Locusts are taken literally to mean devastation of crops in the case of farmers; figuratively as "wicked men and women" for non-farmers; and "Extravagance, misfortune, & ephemeral happiness" by "gypsies".[65]

As food

In some countries, grasshoppers are used as food.[66] In southern Mexico, grasshoppers, known as *chapulines*, are eaten in a variety of dishes, such as in tortillas with chilli sauce.[67] Grasshoppers are served on skewers in some Chinese food markets, like the Donghuamen Night Market.[68] Fried grasshoppers (*walang goreng*) are eaten in the Gunung Kidul Regency, Yogyakarta, Java in Indonesia.[69] In America, the Ohlone burned grassland to herd grasshoppers into pits where they could be collected as food.[70]


Fried grasshoppers from Gunung Kidul, Yogyakarta, Indonesia

It is recorded in the Bible that John the Baptist ate locusts and wild honey (Greek: ἀκρίδες καὶ μέλι ἄγριον, *akrídes kaì méli ágrion*) while living in the wilderness.[71] However, because of a tradition of depicting him as an ascetic, attempts have been made to explain that the *locusts* were in fact a suitably ascetic vegetarian food such as carob beans, notwithstanding the fact that the word *ἀκρίδες* means plainly *grasshoppers*.[72][73]

As pests


Crop pest: grasshopper eating a maize leaf

Grasshoppers eat large quantities of foliage both as adults and during their development, and can be serious pests of arid land and prairies. Pasture, grain, forage, vegetable and other crops can be affected. Grasshoppers often bask in the sun, and thrive in warm sunny conditions, so drought stimulates an increase in grasshopper populations. A single season of drought is not normally sufficient to stimulate a major population increase, but several successive dry seasons can do so, especially if the intervening winters are mild so that large numbers of nymphs survive. Although sunny weather stimulates growth, there needs to be an adequate food supply for the increasing grasshopper population. This means that although precipitation is needed to stimulate plant growth, prolonged periods of cloudy weather will slow nymphal development.[74]

Grasshoppers can best be prevented from becoming pests by manipulating their environment. Shade provided by trees will discourage them and they may be prevented from moving onto developing crops by removing coarse vegetation from fallow land and field margins and discouraging thick growth beside ditches and on roadside verges. With increasing numbers of grasshoppers, predator numbers may increase, but this seldom happens rapidly enough to have much effect on populations. Biological control is being investigated, and spores of the protozoan parasite *Nosema locustae* can be used mixed with bait to control grasshoppers, being more effective with immature insects.[75] On a small scale, neem products can be effective as a feeding deterrent and as a disruptor of nymphal development. Insecticides can be used, but adult grasshoppers are difficult to kill, and as they move into fields from surrounding rank growth, crops may soon become reinfested.[74]

Some grasshopper species, like the Chinese rice grasshopper, are a pest in rice paddies. Ploughing exposes the eggs on the surface of the field, to be destroyed by sunshine or eaten by natural enemies. Some eggs may be buried too deeply in the soil for hatching to take place.[76]

Locust plagues can have devastating effects on human populations, causing famines and population upheavals. They are mentioned in both the Koran and the Bible and have also been held responsible for cholera epidemics, resulting from the corpses of locusts drowned in the Mediterranean Sea and decomposing on beaches.[42] The FAO and other organisations monitor locust activity around the world. Timely application of pesticides can prevent nomadic bands of hoppers from forming before dense swarms of adults can build up.[77] Besides conventional control using contact insecticides,[77] biological pest control using the entomopathogenic fungus *Metarhizium acridum*, which specifically infects grasshoppers, has been used with some success.[78]

In literature

Egyptian hieroglyphs "snḥm"

The Egyptian word for locust or grasshopper was written *snḥm* in the consonantal hieroglyphic writing system. The pharaoh Ramesses II compared the armies of the Hittites to locusts: "They covered the mountains and valleys and were like locusts in their multitude."[79]

One of Aesop's Fables, later retold by La Fontaine, is the tale of *The Ant and the Grasshopper*. The ant works hard all summer, while the grasshopper plays. In winter, the ant is ready but the grasshopper starves. Somerset Maugham's short story "The Ant and the Grasshopper" explores the fable's symbolism via complex framing.[80] Other human weaknesses besides improvidence have become identified with the grasshopper's behaviour.[65] So an unfaithful woman (hopping from man to man) is "a grasshopper" in "Poprygunya", an 1892 short story by Anton Chekhov,[81] and in Jerry Paris's 1969 film *The Grasshopper*.[82][83]

In mechanical engineering

The name "Grasshopper" was given to the Aeronca L-3 and Piper L-4 light aircraft, both used for reconnaissance and other support duties in World War II. The name is said to have originated when Major General Innis P. Swift saw a Piper making a rough landing and remarked that it looked like a "damned grasshopper" for its bouncing progress.[83][84][85]

A grasshopper beam engine, 1847

Grasshopper beam engines were beam engines pivoted at one end, the long horizontal arm resembling the hind leg of a grasshopper. The type was patented by William Freemantle in 1803.[86][87][88]

Notes

a. The symbol is a wordplay on the name Gresham and "grass".[62]

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Manduca quinquemaculata

Manduca quinquemaculata, the **five-spotted hawkmoth**, is a brown and gray hawk moth of the family Sphingidae. The caterpillar, often referred to as the **tomato hornworm**, can be a major pest in gardens; they get their name from a dark projection on their posterior end and their use of tomatoes as host plants. Tomato hornworms are closely related to (and sometimes confused with) the tobacco hornworm *Manduca sexta*. This confusion arises because caterpillars of both species have similar morphologies and feed on the foliage of various plants from the family Solanaceae, so either species can be found on tobacco or tomato leaves. Because of this, the plant on which the caterpillar is found does not indicate its species.

Manduca quinquemaculata

Male - dorsal view

Male - ventral view

Scientific classification

Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Insecta
Order:	Lepidoptera
Family:	Sphingidae
Genus:	*Manduca*
Species:	***M. quinquemaculata***

Binomial name

Manduca quinquemaculata
(Haworth, 1803)[1]

Synonyms

- *Sphinx 5-maculatus* Haworth, 1803
- *Phlegethontius quinquemaculatus*
- *Protoparce quinquemaculatus*

Contents

Range

M. quinquemaculata is found across North America and Australia. The tobacco hornworm, a close relative of the tomato hornworm, tends to dominate the south while tomato hornworms are more prevalent in the northern United States.[2]

Food plants

- *Phlegethontius celeus* Hübner, 1821
- *Protoparce quinquemaculatus wirti* Schaus, 1927

Larva

Tomato hornworms are known to eat various plants from the family Solanaceae, commonly feeding on tomato, eggplant, pepper, tobacco, moonflowers and potato. Females prefer to oviposit on young leaves near the stem of host plants, and early instar caterpillars can often be found here during the day.[3] In the evening or early morning when sunlight is less direct, the caterpillars will feed on more distal leaves.[4]

Adult

Adult diet

Adults feed on nectar from flowering plants including *Datura meteloides,*[5] *Oenothera caespitosa,* and *Mirabilis multiflora.* Most of the food plants they target have large, fragrant white flowers.[6]

Interactions with host plants

Hawkmoths, including *M. quinquemaculata,* are the primary pollinators of *D. meteloides.* The length of the moth's proboscis (around 10 cm), which is an elongated, tubular mouthpart used for sucking and feeding, is well-suited for retrieving nectar from the flowers. Aside from being a host plant for *M. quinquemaculata, D. meteloides* has also been used by humans for its opioid effects. *D. meteloides* contains tropane alkaloids, which are present throughout the plant including in the flowers.[5] These alkaloids have an intoxicating effects on the moth, which displays erratic flight patterns as well as uncoordinated, and often unsuccessful, landing attempts after consuming the nectar. Despite the impairment the nectar causes, the moths have been observed returning to the flowers and consuming more nectar. It has been hypothesized that the “spiked” nectar offers the moths reward beyond just nutrients.[5]

Both *Mirabilis multiflora* and *Oenothera caespitosa* are also dependent on hawkmoths for pollination. *M. quinquemaculata* has been found to feed from *Oenothera caespitosa* first and only later to visit *Mirabilis multiflora,* indicating a preference for the former.[6]

Life cycle

Oviposition

Females lay eggs singly on the surface of host plant leaves in late spring. Larvae hatch after approximately one week.[7] The female decides where to lay eggs based on an assessment of the risk of predation her offspring will face. On the tobacco plant *Nicotiana attenuata,* young leaves close to a plant's stem are more protected from predators and larvae that grow there gain more mass than larvae grown elsewhere on the plant; females prefer to oviposit, or lay their eggs, on these leaves.[3] Eggs are large and range in color from pale green to off-white.[4]

Larva

M. quinquemaculata larvae are large green caterpillars reaching a length of up to 10 cm when fully grown.[7] The caterpillars have a dark, pointed projection on their rear end that earns them the name "hornworm".[7] Although the tomato hornworm, *M. quinquemaculata,* can be confused with the tobacco hornworm, *M. sexta,* the larvae of these species can be distinguished by their lateral markings: tomato hornworms have eight V-shaped white markings with no borders and dark blue or black horns, while tobacco hornworms have seven white diagonal lines with a black border and red horns.[8]

Caterpillars hatch in late spring to early summer. They develop through five instars to reach maturity.[3][7] In warmer climates where the first generation emerges earlier in the year, two generations of caterpillars can coexist in a single summer.[4] Once fully grown, caterpillars fall from their host plants to pupate.[7]

Pupa

Caterpillars pupate in early fall, which means they enter a stage of their life cycle where they become a pupa and undergo transformation into a moth.[7] After pupation, *M. quinquemaculata* overwinter in the soil near their host plants, with adults emerging the following summer.[9][4]

Adults

Adults are large, with a wingspan of up to 13 cm.[7] The wings of the moth are brown and gray with large mottled front wings and smaller hindwings with light and dark zig-zag patterned bands. The abdomens are brown and white with a row of five yellow spots down each side, giving them the name "five-spotted hawkmoth."[10][4] The moths of *M. quinquemaculata* and *M. sexta* can be distinguished by the number of spots on their abdomens.[8]

Shortly after adults emerge from the soil, they mate and females lay their eggs on host plants, renewing the life cycle.[7]

Tomato hornworm larva

closely related tobacco hornworm - note the red horn and lack of V-shaped white markings

Female - dorsal view

Female - ventral view

Relationship with *M. sexta*

M. quinquemaculata and *M. sexta* are both large hawkmoths of the genus *Manduca.* The two species have similar appearances in both larvae and adults and share common food sources, including tobacco.[4][11] Past research, observing that the two species are similar, referred to the two as sister species. However, a recent phylogenetic analysis from Kawahara et al. (2013) found that the two species, though closely related, are not sister species. The authors tracked the ancestral origin of both species to Central America, where the two species diverged from one another.[12]

Pest control

Because the larvae are pests of crop plants such as tomatoes and tobacco, biological control agents and traps have been used to control their populations. Gardeners whose tomato plants are predated by the tomato hornworm pick the caterpillars off of their plants.[4] Some gardeners plant marigolds, which repel the species, near their tomato plants to reduce predation.[13]

Parasites

Braconidae wasp

The parasitoid wasp *Trichogramma* attacks *M. quinquemaculata* eggs. The larvae of the wasp develop in the egg, preventing the development of the caterpillar larvae. *Trichogramma* is a natural enemy of the *M. quinquemaculata* and has also been used as a biological control agent by humans.[14]

A second parasitoid wasp, *Cotesia congregata* of the family Braconidae, also kills *M. quinquemaculata*. Adult females lay their eggs inside the skin of the hornworm caterpillar. After hatching, the wasp larvae use the organs and tissues of the caterpillar as food sources before burrowing out of the skin and pupating on the back and sides of the caterpillar. Once the wasps have emerged from their cocoons, the weakened caterpillar dies. Like the parasitoid wasp mentioned above, these wasps have also been suggested as a means of biological control of the tomato hornworm.[15][16]

closely related tobacco hornworm parasitized by braconid wasp

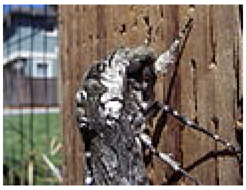
Traps

Adult *M. quinquemaculata* are most active in flight after dark.[10] Early studies found that the moths are attracted to blacklight, which is used as a lure in some traps. Although the traps can be used for research and the moths can be released after capture, traps like these have been suggested as a means of population control. However, one study found that the reduction in population was not strong enough to significantly impact population size.[17]

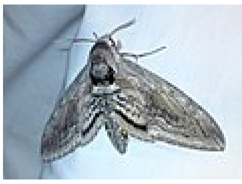
Images

Tomato hornworm larva

M. quinquemaculata diversity



Head detail



Live *M. quinquemaculata*

Tomato worm illuminated with UV on tomato plant

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Integrated pest management

Integrated pest management (IPM), also known as **integrated pest control (IPC)** is a broad-based approach that integrates practices for economic control of pests. IPM aims to suppress pest populations below the economic injury level (EIL). The UN's Food and Agriculture Organization defines IPM as "the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms."[1] Entomologists and ecologists have urged the adoption of IPM pest control since the 1970s.[2] IPM allows for safer pest control.

An IPM boll weevil trap in a cotton field (Manning, South Carolina).

The introduction and spread of invasive species can also be managed with IPM by reducing risks while maximizing benefits and reducing costs.[3][4][5]

Contents

History

Shortly after World War II, when synthetic insecticides became widely available, entomologists in California developed the concept of "supervised insect control".[6] Around the same time, entomologists in the US Cotton Belt were advocating a similar approach. Under this scheme, insect control was "supervised" by qualified entomologists and insecticide applications were based on conclusions reached from periodic monitoring of pest and natural-enemy populations. This was viewed as an alternative to calendar-based programs. Supervised control was based on knowledge of the ecology and analysis of projected trends in pest and natural-enemy populations.

Supervised control formed much of the conceptual basis for the "integrated control" that University of California entomologists articulated in the 1950s. Integrated control sought to identify the best mix of chemical and biological controls for a given insect pest. Chemical insecticides were to be used in the manner least disruptive to biological control. The term "integrated" was thus

synonymous with "compatible." Chemical controls were to be applied only after regular monitoring indicated that a pest population had reached a level (the economic threshold) that required treatment to prevent the population from reaching a level (the economic injury level) at which economic losses would exceed the cost of the control measures.

IPM extended the concept of integrated control to all classes of pests and was expanded to include all tactics. Controls such as pesticides were to be applied as in integrated control, but these now had to be compatible with tactics for all classes of pests. Other tactics, such as host-plant resistance and cultural manipulations, became part of the IPM framework. IPM combined entomologists, plant pathologists, nematologists and weed scientists.

In the United States, IPM was formulated into national policy in February 1972 when President Richard Nixon directed federal agencies to take steps to advance the application of IPM in all relevant sectors. In 1979, President Jimmy Carter established an interagency IPM Coordinating Committee to ensure development and implementation of IPM practices.[7]

Perry Adkisson and Ray F. Smith received the 1997 World Food Prize for encouraging the use of IPM.[8]

Applications

IPM is used in agriculture, horticulture, forestry, human habitations, preventive conservation and general pest control, including structural pest management, turf pest management and ornamental pest management.

Principles

An American IPM system is designed around six basic components:[9]

- **Acceptable pest levels**—The emphasis is on *control*, not *eradication*. IPM holds that wiping out an entire pest population is often impossible, and the attempt can be expensive and unsafe. IPM programmes first work to establish acceptable pest levels, called action thresholds, and apply controls if those thresholds are crossed. These thresholds are pest and site specific, meaning that it may be acceptable at one site to have a weed such as white clover, but not at another site. Allowing a pest population to survive at a reasonable threshold reduces selection pressure. This lowers the rate at which a pest develops resistance to a control, because if almost all pests are killed then those that have resistance will provide the genetic basis of the future population. Retaining a significant number of unresistant specimens dilutes the prevalence of any resistant genes that appear. Similarly, the repeated use of a single class of controls will create pest populations that are more resistant to that class, whereas alternating among classes helps prevent this.
- **Preventive cultural practices**—Selecting varieties best for local growing conditions and maintaining healthy crops is the first line of defense. Plant quarantine and 'cultural techniques' such as crop sanitation are next, e.g., removal of diseased plants, and cleaning pruning shears to prevent spread of infections. Beneficial fungi and bacteria are added to the potting media of horticultural crops vulnerable to root diseases, greatly reducing the need for fungicides.
- **Monitoring**—Regular observation is critically important. Observation is broken into inspection and identification.[10] Visual inspection, insect and spore traps, and other methods are used to monitor pest levels. Record-keeping is essential, as is a thorough knowledge of target pest behavior and reproductive cycles. Since insects are cold-blooded, their physical development is dependent on area temperatures. Many insects have had their development cycles modeled in terms of degree-days. The degree days of an environment determines the optimal time for a specific insect outbreak. Plant pathogens follow similar patterns of response to weather and season.
- **Mechanical controls**—Should a pest reach an unacceptable level, mechanical methods are the first options. They include simple hand-picking, barriers, traps, vacuuming and tillage to disrupt breeding.
- **Biological controls**—Natural biological processes and materials can provide control, with acceptable environmental impact, and often at lower cost. The main approach is to promote beneficial insects that eat or parasitize target pests. Biological insecticides, derived from naturally occurring microorganisms (*e.g.*—*Bt*, entomopathogenic fungi and entomopathogenic nematodes), also fall in this category. Further 'biology-based' or 'ecological' techniques are under evaluation.
- **Responsible use**—Synthetic pesticides are used as required and often only at specific times in a pest's life cycle. Many newer pesticides are derived from plants or naturally occurring substances (*e.g.*—nicotine, pyrethrum and insect juvenile hormone analogues), but the toxophore or active component may be altered to provide increased biological activity or stability. Applications of pesticides must reach their intended targets.

> Matching the application technique to the crop, the pest, and the pesticide is critical. The use of low-volume spray equipment reduces overall pesticide use and labor cost.

An IPM regime can be simple or sophisticated. Historically, the main focus of IPM programmes was on agricultural insect pests.[11] Although originally developed for agricultural pest management, IPM programmes are now developed to encompass diseases, weeds and other pests that interfere with management objectives for sites such as residential and commercial structures, lawn and turf areas, and home and community gardens.

Process

IPM is the selection and use of pest control actions that will ensure favourable economic condition, ecological and social consequences[12] and is applicable to most agricultural, public health and amenity pest management situations. The IPM process starts with monitoring, which includes inspection and identification, followed by the establishment of economic injury levels. The economic injury levels set the economic threshold level. That is the point when pest damage (and the benefits of treating the pest) exceed the cost of treatment.[13] This can also be an action threshold level for determining an unacceptable level that is not tied to economic injury. Action thresholds are more common in structural pest management and economic injury levels in classic agricultural pest management. An example of an action threshold is one fly in a hospital operating room is not acceptable, but one fly in a pet kennel would be acceptable. Once a threshold has been crossed by the pest population action steps need to be taken to reduce and control the pest. Integrated pest management employs a variety of actions including cultural controls such as physical barriers, biological controls such as adding and conserving natural predators and enemies of the pest, and finally chemical controls or pesticides. Reliance on knowledge, experience, observation and integration of multiple techniques makes IPM appropriate for organic farming (excluding synthetic pesticides). These may or may not include materials listed on the Organic Materials Review Institute (OMRI)[14] Although the pesticides and particularly insecticides used in organic farming and organic gardening are generally safer than synthetic pesticides, they are not always more safe or environmentally friendly than synthetic pesticides and can cause harm.[15] For conventional farms IPM can reduce human and environmental exposure to hazardous chemicals, and potentially lower overall costs.

Risk assessment usually includes four issues: 1) characterization of biological control agents, 2) health risks, 3) environmental risks and 4) efficacy.[16]

Mistaken identification of a pest may result in ineffective actions. E.g., plant damage due to over-watering could be mistaken for fungal infection, since many fungal and viral infections arise under moist conditions.

Monitoring begins immediately, before the pest's activity becomes significant. Monitoring of agricultural pests includes tracking soil/planting media fertility and water quality. Overall plant health and resistance to pests is greatly influenced by pH, alkalinity, of dissolved mineral and oxygen reduction potential. Many diseases are waterborne, spread directly by irrigation water and indirectly by splashing.

Once the pest is known, knowledge of its lifecycle provides the optimal intervention points.[17] For example, weeds reproducing from last year's seed can be prevented with mulches and pre-emergent herbicide.

Pest-tolerant crops such as soybeans may not warrant interventions unless the pests are numerous or rapidly increasing. Intervention is warranted if the expected cost of damage by the pest is more than the cost of control. Health hazards may require intervention that is not warranted by economic considerations.

Specific sites may also have varying requirements. E.g., white clover may be acceptable on the sides of a tee box on a golf course, but unacceptable in the fairway where it could confuse the field of play.[18]

Possible interventions include mechanical/physical, cultural, biological and chemical. Mechanical/physical controls include picking pests off plants, or using netting or other material to exclude pests such as birds from grapes or rodents from structures. Cultural controls include keeping an area free of conducive conditions by removing waste or diseased plants, flooding, sanding,

and the use of disease-resistant crop varieties.[12] Biological controls are numerous. They include: conservation of natural predators or augmentation of natural predators, sterile insect technique (SIT).[19]

Augmentation, inoculative release and inundative release are different methods of biological control that affect the target pest in different ways. Augmentative control includes the periodic introduction of predators.[20][21][22][23][24] With inundative release, predators are collected, mass-reared and periodically released in large numbers into the pest area.[25][26][27] This is used for an immediate reduction in host populations, generally for annual crops, but is not suitable for long run use.[28] With inoculative release a limited number of beneficial organisms are introduced at the start of the growing season. This strategy offers long term control as the organism's progeny affect pest populations throughout the season and is common in orchards.[28][29] With seasonal inoculative release the beneficials are collected, mass-reared and released seasonally to maintain the beneficial population. This is commonly used in greenhouses.[29] In America and other western countries, inundative releases are predominant, while Asia and the eastern Europe more commonly use inoculation and occasional introductions.[28]

The sterile insect technique (SIT) is an area-wide IPM program that introduces sterile male pests into the pest population to trick females into (unsuccessful) breeding encounters, providing a form of birth control and reducing reproduction rates.[19] The biological controls mentioned above only appropriate in extreme cases, because in the introduction of new species, or supplementation of naturally occurring species can have detrimental ecosystem effects. Biological controls can be used to stop invasive species or pests, but they can become an introduction path for new pests.[30]

Chemical controls include horticultural oils or the application of insecticides and herbicides. A green pest management IPM program uses pesticides derived from plants, such as botanicals, or other naturally occurring materials.

Pesticides can be classified by their modes of action. Rotating among materials with different modes of action minimizes pest resistance.[12]

Evaluation is the process of assessing whether the intervention was effective, whether it produced unacceptable side effects, whether to continue, revise or abandon the program.[31]

Southeast Asia

The Green Revolution of the 1960s and '70s introduced sturdier plants that could support the heavier grain loads resulting from intensive fertilizer use. Pesticide imports by 11 Southeast Asian countries grew nearly sevenfold in value between 1990 and 2010, according to FAO statistics, with disastrous results. Rice farmers become accustomed to spraying soon after planting, triggered by signs of the leaf folder moth, which appears early in the growing season. It causes only superficial damage and doesn't reduce yields. In 1986, Indonesia banned 57 pesticides and completely stopped subsidizing their use. Progress was reversed in the 2000s, when growing production capacity, particularly in China, reduced prices. Rice production in Asia more than doubled. But it left farmers believing more is better—whether it's seed, fertilizer, or pesticides.[32]

The brown planthopper, *Nilaparvata lugens*, the farmers' main target, has become increasingly resistant. Since 2008, outbreaks have devastated rice harvests throughout Asia, but not in the Mekong Delta. Reduced spraying allowed natural predators to neutralize planthoppers in Vietnam. In 2010 and 2011, massive planthopper outbreaks hit 400,000 hectares of Thai rice fields, causing losses of about $64 million. The Thai government is now pushing the "no spray in the first 40 days" approach.[32]

By contrast early spraying kills frogs, spiders, wasps and dragonflies that prey on the later-arriving and dangerous planthopper and produced resistant strains. Planthoppers now require pesticide doses 500 times greater than originally. Overuse indiscriminately kills beneficial insects and decimates bird and amphibian populations. Pesticides are suspected of harming human health and became a common means for rural Asians to commit suicide.[32]

In 2001, scientists challenged 950 Vietnamese farmers to try IPM. In one plot, each farmer grew rice using their usual amounts of seed and fertilizer, applying pesticide as they chose. In a nearby plot, less seed and fertilizer were used and no pesticides were applied for 40 days after planting. Yields from the experimental plots was as good or better and costs were lower, generating 8% to 10% more net income. The experiment led to the "three reductions, three gains" campaign, claiming that cutting the use of seed, fertilizer and pesticide would boost yield, quality and income. Posters, leaflets, TV commercials and a 2004 radio soap opera that featured a rice farmer who gradually accepted the changes. It didn't hurt that a 2006 planthopper outbreak hit farmers using insecticides harder than those who didn't. Mekong Delta farmers cut insecticide spraying from five times per crop cycle to zero to one.

The Plant Protection Center and the International Rice Research Institute (IRRI) have been encouraging farmers to grow flowers, okra and beans on rice paddy banks, instead of stripping vegetation, as was typical. The plants attract bees and a tiny wasp that eats planthopper eggs, while the vegetables diversify farm incomes.[32]

Agriculture companies offer bundles of pesticides with seeds and fertilizer, with incentives for volume purchases. A proposed law in Vietnam requires licensing pesticide dealers and government approval of advertisements to prevent exaggerated claims. Insecticides that target other pests, such as *Scirpophaga incertulas* (stem borer), the larvae of moth species that feed on rice plants allegedly yield gains of 21% with proper use.[32]

See also

- Agroecology
- Agronomy
- Biodynamic agriculture
- Endangered arthropod
- Forest integrated pest management
- International Organization for Biological Control
- Pesticide application
- Professional Landcare Network (PLANET)
- Push-pull technology
- Soil contamination
- Sustainable agriculture

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